Klinik für Zoo-, Heim- und Wildtiere

der Vetsuisse-Fakultät Universität Zürich

Direktor: Prof. Dr. med. vet. Jean-Michel Hatt

Arbeit unter wissenschaftlicher Betreuung von

Prof. Dr. med. vet. Jean-Michel Hatt

Prof. Dr. med. vet. Marcus Clauss

Body Condition Scores in European Zoo Elephants

Inaugural Dissertation

Zur Erlangung der Doktorwürde der

Vetsuisse-Fakultät Universität Zürich

vorgelegt von

Christian Schiffmann

Tierarzt

von Homberg, Bern

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Body Condition Scores der Zooelefanten Europas

Zusammenfassung

Zur Beurteilung der Verfassung von Zootieren wurden verschiedene Body Condition Scoring (BCS) Protokolle entwickelt. Diese werden nach Vorgehen als "composite", "algorithm" und "overview" klassifiziert. Anwendbarkeit und Verlässlichket der Ansätze wurden beim Scoring einer Bilderzusammenstellung Afrikanischer (*Loxodonta africana*) bzw. Asiatischer (*Elephas maximus*) Zooelefanten durch Studenten untersucht. Das „overview" Protokoll wies die höchste Trennschärfe auf. Darauf basierend wurde eine Erhebung zum BCS der Zooelefanten Europas durchgeführt. Dabei konnten 192 Afrikanische und 326 Asiatische Elefanten (97% der Population) beurteilt werden. Mit 56% lag die Mehrheit der Elefanten im Scorebereich 7-10 von maximal 10. Adulte Asiatische wiesen signifikant tiefere Werte als Afrikanische Elefanten auf. Im Vergleich zu Stichproben freilebender Populationen lagen die Scores der Zooelefanten unabhängig von Art, Alter und Geschlecht signifikant höher. Verglichen mit anderen Elefantenpopulationen in Menschenobhut scheinen die Zooelefanten Europas aber weniger übergewichtig. Bei adulten Asiatischen Weibchen wiesen züchtende Elefanten tiefere Werte als nicht-züchtende auf. Ein langfristiges Gewichtsmanagement der Zooelefanten mittels BCS wird empfohlen.

Stichworte: Zooelefanten, Body Condition Scoring

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Body Condition Scores in European Zoo Elephants

Summary

Various body condition scoring (BCS) methods have been developed in zoo animals. Composite, algorithm and overview protocols are distinguished. To compare their practicability and consistency, a test was conducted with students scoring an equal number of African (*Loxodonta africana*) and Asian elephant (*Elephas maximus*) photographs. The overview protocol led to the highest differentiation of elephant condition. Based on these finding, a population-wide evaluation of body condition of European zoo elephants was conducted. The assessment included 192 African and 326 Asian elephants (97% of the population). The majority of elephants were in the upper score categories with 56% of adults assessed in the range 7-10 out of 10. Adult Asian had significantly lower BCS than African elephants. Comparison with samples of free-ranging populations revealed lower scores in free-ranging elephants independent of species, age and sex. Compared to previous reports from captive populations, European zoo elephants are less obese. In adult Asian females, BCS was correlated to their breeding status with lower scores in current breeders. Further attention to zoo elephant weight management is recommended with longitudinal monitoring by body condition scoring.

Keywords: zoo elephants, body condition scoring

Visual body condition scoring in zoo animals – composite, algorithm and overview approaches in captive Asian and African elephants

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Visual body condition scoring in zoo animals – composite, algorithm and overview approaches in captive Asian and African elephants

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Abstract:
Various body condition scoring (BCS) methods have been developed as management tools in zoo animal husbandry. In contrast to BCS for farm animals, where visual and palpable features are used, these protocols are mainly restricted to visual cues. Considering their inherent subjectivity, such methods face scepticism as their reliability is questioned. In terms of their respective methodology, composite BCS (where individual body regions are scored and a sum or mean is calculated), algorithm BCS (where a score is achieved by following a flow chart) and overview BCS protocols (where a score is given based on overall appearance) can be distinguished. In order to compare their practicability and consistency, we conducted a test with veterinary students (n=18) scoring an equal number (n=15) of African (*Loxodonta africana*) and Asian elephant (*Elephas maximus*) photographs using three different protocols. The composite approach showed least inter-observer consistency, while the overview protocol led to the highest differentiation of individual elephant condition. When regularly assessed, visual body condition scoring may serve as an important tool for the health surveillance and complete the medical history of individual zoo animals. Nonetheless, a validation process for each protocol developed should be carried out before its application. Further research might concentrate on long-term, individual-based body condition monitoring, using archives of standardised photographs.

Introduction

The assessment of body condition is an important tool in various animal management systems, whether one manages free-ranging populations, domesticated farm animals or captive zoo animal species. While economic interest motivates the practice in production animals, animal health issues are the motivation in scoring pets (Laflamme 2012). A high proportion of companion animals suffer from obesity (Laflamme 2012), and obesity has been a concern in zoo animal husbandry as well. Under the conditions of captivity several wildlife species are known to be prone to obesity (e.g. equids (Bray and Edwards 1999), tapirs (Clauss et al. 2009), rhinos (Clauss et al. 2005), elephants (Morfeld et al. 2014) and monogastric primates (Dierenfeld 1997; Terranova et al. 1997; Videan et al. 2007)), but there are also examples such as giraffe (Potter and Clauss 2005) and moose (Clauss et al. 2002), in which poor body conditions seem to occur more frequently. Moreover, body condition scoring systems are used extensively by ecologists investigating wild populations and their interaction with restricted resources or changing environments (DelGiudice et al. 2011; Lane et al. 2014; Carpio et al. 2015; McWilliams and Wilson 2015).

In order to achieve the most accurate estimation of an animal´s physical condition, a number of different scoring methods have been developed, such as the kidney fat index, bone marrow fat index (Jakob et al. 1996; Cook et al. 2007), bioelectrical impedance analysis, and morphometric measurements such as weight, size, circumferences and ratios from these values (Barthelmess et al. 2006; Pitt et al. 2006; Peig and Green 2009). Production and hunted animals can be scored by invasive non-repeatable techniques at slaughter, including fresh-carcass weight or fat indices, and also with non-invasive methods such as morphometric measurements and visual scores. For the monitoring of pets, only non-invasive repeatable techniques seem adequate. Although post mortem information is important in zoo animals, *in vivo* information is required to facilitate the optimisation of care and management circumstances (Ward et al. 1999).

Individuals typically differ in body mass, depending not only on their nutritional status, but on their phenotype. To account for this, mass measurements are typically related to a geometric body measure such as length or area. In humans this is done by the calculation of the so-called body mass index (BMI), a ratio of body mass and stature in metres squared (e.g. Foster et al. 2012). In animals, various species-specific measurements have been used in order to obtain similar ratios, using body mass against, for example, total length in geese (Halse 1984), limb length in kangaroos (Moss and Croft 1999), carapace length in tortoises (Furrer et al. 2004), wing length in penguins (Clements and Sanchez 2015), body length in raccoons (McWilliams and Wilson 2015), and shoulder height in rhinos (Heidegger et al. 2016). While these studies tried to readjust body mass using further geometric measurements, formulae have been developed to calculate body mass from body length, shoulder height and chest girth in Asian elephants (Kurt and Nettasinghe 1968; Sreekumar and Nirmalan 1989).

These methods show variable practicability depending on the purpose of the assessment and the population concerned. Most of them are post mortem measurements and thus not helpful for the monitoring of live animals. For the latter, a less invasive technique such as the body condition score (BCS) is warranted. While such a system may consider palpable and visual cues in domesticated or tamed individuals, it is restricted to the visually detectable ones in most wildlife species (Bray and Edwards 1999). Lacking these limitations, the existence of an established system for almost every domesticated animal species seems unsurprising (cattle (Wildman et al. 1982), horses (Henneke et al. 1983; Kienzle and Schramme 2004), sheep (Russel 1984), pigs (DEFRA 1998), dogs (Laflamme 1997), buffaloes (Alapati et al. 2010) and goats (Vieira et al. 2015)).

Focusing on wild and zoo animals, a visual body condition scoring system will not be viable for every species. For example, birds are usually not scored by a visual method because their plumage covers benchmarks of the body shape such as bony protuberances and muscular contours. Nevertheless, the usefulness of such an index has been demonstrated in geese (Owen 1981) and Magellanic penguin (*Spheniscus magellanicus*) (Clements and Sanchez 2015). The extraordinarily flat and dense coat of geese and penguins facilitates the use of a visual score in these species.

In mammalian species, visual characteristics alone do not necessarily provide reliable results, either. According to Gerhart et al. (1996), the dense hair coat of caribou prevents any visual evaluation of body contours, while in ungulates originating from warmer climatic regions the practicability of visual body condition scoring systems has been extensively documented (Riney 1960; Gallivan et al. 1995; Ezenwa et al. 2009; Wright et al. 2011; Taylor et al. 2013). Animals with short or no hair are obviously well-suited for an assessment based on visual cues. Thus multiple species-specific protocols have been developed and shown to be useful under field conditions for rhinos (Keep 1971; Reuter and Adcock 1998, Heidegger et al. 2016), tapirs (Clauss et al. 2009) and elephants (Poole 1989; Wemmer et al. 2006; Fernando et al. 2009; Morfeld et al. 2014, 2016; Wijeyamohan et al. 2014).

Independent of the species investigated, the benefits of a visual BCS system are its practicability, simplicity and the low costs. Moreover, according to Bray and Edwards (2001), Reppert et al. (2011) and Clements and Sanchez (2015), a numerical BCS can facilitate communication amongst care teams and hence improve management of an animal species in a zoo setting.

The visual approach

Following the structure of the earliest established scoring systems for farm animals (Wildman et al. 1982; Henneke et al. 1983), most of the existing protocols consist of five or more categories, where a score of one represents the poorest and five the highest body condition. For each score, the indices provide a description, commonly combined with an example photograph or drawing. In zoo animal species, the pictorial part is often emphasised due to its practicability under field conditions, where time to read is often not ensured and the individual under investigation has to be categorised at a glance (Riney 1960; Fernando et al. 2009; Morfeld et al. 2014). Depending on the level of differentiation, a system may allow increments at 0.5-intervals or full numbers only. The latter is often the case in BCS comprising more than five categories, while the former is common in five-point scales. Besides the direct assessment, describing a category for every single score, some indices propose an indirect evaluation. In doing so, every other condition is defined by lying between the two neighbouring ones (e.g. Fernando et al. 2009).

Because of its acceptance as a tool in the weight management of zoo animals (Ward et al. 1999; Bray and Edwards 1999), several species-specific visual scoring systems have already been developed. Their similarities and differences are listed in Table 1. With respect to practicability of a visual scoring system, the body areas evaluated need to be easily visible. This is shown in the pioneering protocol by Riney (1960) as well as in the subsequent indices developed for further wild and zoo animal species (Reuter and Adcock 1998; Wemmer et al. 2006; Dierenfeld et al. 2007; Clauss et al. 2009; Fernando et al. 2009; Wright et al. 2011; Morfeld et al. 2014; Wijeyamohan et al. 2014). All these systems mainly emphasise anatomical characteristics of the hind half of the body such as tail head, backbone, pelvic bone and ribs (see also Table 1). Several species-specific indices have been adapted and optimised by validation studies, whereby regions showing high correlation with direct or indirect quantitative measurements of body fat remained in the protocol, while others were excluded. For example, Morfeld et al. (2014) investigated body areas in African elephants previously suggested by Wemmer et al. (2006) to be relevant in Asian elephants. These authors correlated the visual scores with subcutaneous fat measurements in the same animals, and excluded regions for which no strong correlation could be determined (e.g. head, shoulders). According to this methodology, any scoring system should have gone through such a validation process in order to ensure reliable and consistent results (Cook et al. 2001b; Barthelmess et al. 2006; Pitt et al. 2006; Peig et al. 2009). Scoring body areas not highly correlating with an established gold standard might provide misleading results (Cook et al. 2001b). Apart from the aforementioned species-specific morphometric measurements, several validation techniques can be used in a number of taxa. These are the determination of the amount of subcutaneous fat by ultrasonography (Cook et al. 2001a; Stringer et al. 2010; DelGiudice et al. 2011; Reppert et al. 2011; Treiber et al. 2012; Morfeld et al. 2014), bioelectrical impedance analysis (Barthelmess et al. 2006; Pitt et al. 2006), measurement of serum triglyceride levels (Morfeld et al. 2016), direct measurement of body fat content (Cook et al. 2001b, 2007) or the amount of kidney fat (Ezenwa et al. 2009; Carpio et al. 2015). In addition to limitations due to species-specific characteristics (mainly thick and dense hair) covering the critical anatomical benchmarks, visual scoring can be influenced by various factors. These include the intestinal tract filling and hydration status (Reuter and Adcock 1998), the reproductive stage in females (Dierenfeld et al. 2007; Ezenwa et al. 2009; Reppert et al. 2011) or an increased inter-observer variability due to the subjective character of the technique. The latter can be

Table 1. Overview of specific body condition score protocols published for wild and zoo animal species.

Species	Critical body areas	Body regions scored individually	Defined categories (range of mean score)	Example pictures/ drawings provided	Reference
Barnacle geese (*Branta leucopsis*)	abdominal profile	– (only one single area scored)	4 (1–4)	yes	Owen (1981)
Magellanic penguin (*Spheniscus magellanicus*)	pectoral muscle, keel, ventrum, back, hips, furcula, shoulder	no	5 (1–5)	yes	Clements et al. (2015)
Cheetah (*Acinonyx jubatus*)	neck, shoulders, abdomen, tail head, pelvis, ribs	no	5 (1–5)	yes	Dierenfeld et al. (2007)
Cheetah (*Acinonyx jubatus*)	shoulder, torso, topline, point of hip, hip angle, tail head, point of buttocks, hind leg	no	9 (1–9)	yes	Reppert et al. (2011)
Kinkajou (*Potos flavus*)	ribs, abdomen, hips, shoulder, tail, skull	no	5 (1–5)	yes (but only partially)	Wright and Edwards (2009)
Polar bear (*Ursus maritimus*)	vertebrae, ribs, hip bones	no	5 (skinny, thin, average, fat, very fat)	yes	Stirling et al. (2008)
Black rhinoceros (*Diceros bicornis*)	neck, shoulder, ribs, spine, rump, abdomen, tail base	yes (not imperative, but recommended)	5 (1–5)	yes	Reuter and Adcock (1998)
Greater one-horned rhinoceros (*Rhinoceros unicornis*)	neck, shoulder, ribs, spine, abdomen, rump, tail base	yes	5 (1–5)	yes	Heidegger et al. (2016)
Tapirs (*Tapirus indicus* and *Tapirus terrestris*)	ribs, back, neck, shoulders, tail head, hips	no	5 (1–5)	yes	Clauss et al. (2009)
Baird´s tapir (*Tapirus bairdii*)	head, neck, shoulder, ribs, spine, pelvis	yes	25 (6–30)	yes	Pérez-Flores et al. (2016)
Various ungulate species	tail, pelvic girdle, croup, backbone, ribs	no	3 (good, medium, poor)	yes	Riney (1960)
African buffalo (*Syncerus caffer caffer*)	ribs, spine, hips, tail, coat	yes	5 (1–5)	no	Ezenwa et al. (2009)
Eastern bongo (*Tragelaphus eurycerus isaaci*)	neck, shoulders, withers, loin, back, tail head, hips, ribs	no	5 (1–5)	yes	Wright et al. (2011)
Greater kudu (*Tragelaphus strepsiceros*)	neck, shoulder, ribs, back, hip, tail head	no	5 (1–5)	yes	Taylor et al. (2013)
Giant anteaters (*Myrmecophaga tridactyla)*	neck, shoulder, hip, tail, head	no	5 (1–5)	yes	Clark et al. (2016)
Large hairy armadillo (*Chaetophractus villosus*)	jaw, body shell, hips, thighs	no	5	yes	Clark et al. (2016)
Yellow/six-banded armadillo (*Euphractus sexcinctus*)	jaw, body shell, hips, thighs	no	5	yes	Clark et al. (2016)
Southern three-banded armadillo (*Tolypeutes matacus*)	jaw, body shell, hips, thighs	no	5	yes	Clark et al. (2016)
Aardvarks (*Orycteropus afer*)	neck, shoulder, hip, tail head	no	5 (1–5)	yes	Clark et al. (2016)
Dromedary camel (*Camelus dromedaries*)	ribs, ischial and coxal tuberosities, scapula, vertebrae, flank, recto-genital zone	no	6 (0–5)	yes	Faye et al. (2001)
African elephant (*Loxodonta africana*)	shoulder blade, pelvic bone, backbone, belly	no	6 (1–6)	no	Poole (1989)
African elephant (*Loxodonta africana*)	backbone, pelvic bone, ribs	no	5 (1–5)	yes	Morfeld et al. (2014)
Asian elephant (*Elephas maximus*)	head, scapula, ribs, flank, lumbar vertebrae, pelvic bone	yes	12 (0–11)	yes (but only partially)	Wemmer et al. (2006)
Asian elephant (*Elephas maximus*)	ribs, shoulder and pelvic girdle, backbone, neck	no	11 (0–10)	yes	Fernando et al. (2009)
Asian elephant (*Elephas maximus*)	ribs, scapula, pelvic bone, vertebral column	no	10 (1–10)	yes	Wijeyamohan et al. (2014)
Asian elephant (*Elephas maximus*)	backbone, pelvic bone, ribs	no	5 (1–5)	yes	Morfeld et al. (2016)

Table 2. Overview of reported correlation patterns of visual scoring systems with other body condition indices. *c:* investigated animals live in captivity, *f:* free-ranging individuals were investigated.

Species	Correlating body condition index	Type of correlation	Remarks	Reference
Barnacle geese (*Branta leucopsis*)	weight/wing length ratio	positive, linear	–	Owen (1981)
Magellanic penguin (*Spheniscus magellanicus*)	weight/wing length ratio	positive	–	Clements et al. (2015)
Cheetah (*Acinonyx jubatus*)	body mass	positive, linear	significant only in adult individuals	Reppert et al. (2011)
Polar bear (*Ursus maritimus*)	mass/length^2 ratio	positive	significant	Stirling et al. (2008)
Polar bear (*Ursus maritimus*)	adipose lipid content	positive	significant	Stirling et al. (2008)
Greater one-horned rhinoceros (*Rhinoceros unicornis*)	body mass/shoulder height ratio	positive	–	Heidegger et al. (2016)
Baird´s tapir (*Tapirus bairdii*)	neck circumference	positive	significant	Pérez-Flores et al. (2016)
Baird´s tapir (*Tapirus bairdii*)	thorax circumference	positive	significant	Pérez-Flores et al. (2016)
African buffalo (*Syncerus caffer caffer*)	kidney fat	positive	not detected in females	Ezenwa et al. (2009)
African buffalo (*Syncerus caffer caffer*)	haematocrit	positive	–	Ezenwa et al. (2009)
Yellow/six-banded armadillo (*Euphractus sexcinctus*)	body mass	positive	–	Clark et al. (2016)
African elephant (*Loxodonta africana*)	subcutaneous fat thickness	positive	investigation on female elephants only; strongest correlation for the vertebral ridge	Morfeld et al. (2014)
Asian elephant (*Elephas maximus*)	subcutaneous fat thickness	positive, linear	measured by ultrasound	Treiber et al. (2012)
Asian elephant (*Elephas maximus*)	muscle and muscle + fat thickness	positive, linear	measured by ultrasound	Treiber et al. (2012)
Asian elephant (*Elephas maximus*)	weight/morphometric measurement ratios	positive	measurements taken: height, neck girth, chest girth, hind girth	Wijeyamohan et al. (2014)
Asian elephant (*Elephas maximus*)	skin fold measures	positive	various hanging skin folds measured	Wijeyamohan et al. (2014)
Asian elephant (*Elephas maximus*)	serum triglyceride levels	positive	significant, except for the scores 2 and 3	Morfeld et al. (2016)

minimised if scoring is conducted by a single person (Stringer et al. 2010). Besides the validation of visual-based scoring systems, their correlation patterns with further body condition indices have been investigated and reported (for an overview see Table 2). Furthermore, researchers have succeeded in demonstrating correlation patterns of various parameters with visual body condition scores (compiled in Table 3). Once developed and validated, a visual body condition scoring system can be applied by direct observation or the evaluation of pictorial documents (Ward et al. 1999; Morfeld et al. 2014; Wijeyamohan et al. 2014). Using the latter indirect method of observation, standardisation of the photographs investigated should be considered, in order to allow a reliable assessment (Morfeld et al. 2014). The required level of standardisation depends on the purpose of the study and the species-specific recognisability of the critical body regions (Fernando et al. 2009; Reppert et al. 2011; Morfeld et al. 2014). Apart from differences concerning validation and kind of observation, indices do vary in the way the BCS is obtained. This can be demonstrated in elephants.

Comparison of visual BCS approaches

Composite body condition scoring

Following the protocol by Wemmer et al. (2006), six anatomically distinct characteristics are point-scored and subsequently totalled to obtain the index (Table 1). Thus, each body area is given the same influence on the mean score, with the exception of the flank region, contributing at most one point. A similar approach is to score each body region separately using the entire scale (most often 1–5) with subsequent calculation of a mean value. This has been applied in rhinos by Reuter and Adcock (1998) and Heidegger et al. (2016).

Algorithm body condition scoring

In contrast, Morfeld et al. (2014) and Wijeyamohan et al. (2014) presented an algorithm or flowchart-like guide, emphasising the ribs, scapula and pelvic bone, while the backbone is used for subordinate staging. Therefore, if ribs are visible in an elephant, the flow chart leads to a BCS of 1 independently of the backbone´s

Table 3. Overview of reported correlation patterns of visual body condition scores with other parameters in free-ranging (*f*) and captive (*c*) individuals.

Species	Correlating parameters	Type of correlation	Remarks	Reference
Barnacle geese (*Branta leucopsis*) *f*	feeding on high-energy foods	positive	correlation demonstrated in both directions (BCS increases when food available)	Owen (1981)
Pink-footed geese (*Anser brachyrhynchus*) *f*	harshness of preceding winter	negative	–	Clausen et al. (2015)
Pink-footed geese (*Anser brachyrhynchus*) *f*	individual spring-fattening rates	inversely proportional	only in early spring	Clausen et al. (2015)
Polar bear (*Ursus maritimus*) *f*	season	higher in autumn	except females with cubs	Stirling et al. (2008)
Polar bear (*Ursus maritimus*) *f*	female reproductive status	adult females with cubs in poorer condition than solitary ones	–	Stirling et al. (2008)
Eastern black rhinoceros (*Diceros bicornis michaeli*) *c*	female reproductive status	higher in nulliparous females compared to parous ones	European zoos	Edwards et al. (2015)
Greater one-horned rhinoceros (*Rhinoceros unicornis*) *c*	total estimated dry amount of diet	positive	–	Heidegger et al. (2016)
Greater one-horned rhinoceros (*Rhinoceros unicornis*) *c*	amount of fruits and vegetables in diet	positive	correlation approached significance	Heidegger et al. (2016)
Tapirs (*Tapirus indicus, Tapirus terrestris*) *c*	digestible energy intake	positive	–	Clauss et al. (2009)
Tapirs (*Tapirus indicus, Tapirus terrestris*) *c*	faecal consistency	negative (softer faeces in tapirs with higher BCS)	–	Clauss et al. (2009)
Tapirs (*Tapirus indicus, Tapirus terrestris*) *c*	occurrence of colic	positive	small sample size (four tapirs)	Clauss et al. (2009)
Baird´s tapir (*Tapirus bairdii*) *c* and *f*	captive vs free-ranging	higher in captive compared to free-ranging tapirs	–	Pérez-Flores et al. (2016)
Impalas (*Aepyceros melampus*) *f*	season	poor in winter and spring, good in summer	variation was clearest in lambs and yearlings; nursing females showed a contrary correlation pattern	Gallivan et al. (1995)
Moose (*Alces alces*) *f*	sex	lower in males compared to females	might depend on seasonal activity patterns	DelGuidice et al. (2011)
Greater kudu (*Tragelaphus strepsiceros*) *c*	dry matter intake and intake of metabolisable energy	positive	small sample size	Taylor et al. (2013)
Aardvarks (*Orycteropus afer*) *c*	amount of dry matter offered	negative	small sample size	Clark et al. (2016
African elephant (*Loxodonta africana*) *f*	stage of musth	body condition decreases during musth phase	–	Poole (1989)
African elephant (*Loxodonta africana*) *f*	duration of musth	negative, linear	–	Poole (1989)
African elephant (*Loxodonta africana*) *c and f*	captive vs free-ranging	significantly higher in captive elephants	investigation on female elephants only	Morfeld et al. (2014)
Asian elephant (*Elephas maximus*) *f*	season	decrease in body condition during dry season	significant differences between age-classes	Ramesh et al. (2011)
Asian elephant (*Elephas maximus*) *f*	sex	lower body condition in males	demonstrated for adult elephants only	Ramesh et al. (2011)
Asian elephant (*Elephas maximus*) *c*	sex	higher scores in females	–	Morfeld et al. (2016)
Asian elephant (*Elephas maximus*) *c*	staff-directed walking exercise	decreased risk for higher scores	only significant if exercise exceeds 14 hours per week	Morfeld et al. (2016)
Asian elephant (*Elephas maximus*) *c*	unpredictable feeding schedule	decreased risk for higher scores	–	Morfeld et al. (2016)
Asian elephant (*Elephas maximus*) *c*	diversity in feeding methods	increased risk for higher scores	–	Morfeld et al. (2016)
Asian elephant (*Elephas maximus*) *c*	duration of musth	positive	–	Somgird et al. (2016)

Table 4. Modifications made to the original body condition scoring protocols (Wemmer et al. 2006, Fernando et al. 2009, Morfeld et al. 2014, Wijeyamohan et al. 2014) for their application in the test of the different scoring approaches performed in the present study.

Approach of the scoring system	Author of original protocol	Species	Modification for application in test	Potential alterations of the outcomes
Composite	Wemmer et al. (2006)	Asian elephant (*Elephas maximus*)	Flank area, which was weighted by one point only in the original paper and showed least correlation with subcutaneous fat measurements according to Morfeld et al. (2014), was excluded. Thus the range of the score was reduced from 0–11 to 0–10.	A higher reliability in the scores might be reached.
Algorithm	Morfeld et al. (2014)	African elephant (*Loxodonta africana*)	Addition of score 0 for extremely emaciated elephants. Moreover the five categories were subdivided with the stages in between in accordance to Wijeyamohan et al. (2014). Thus the score range was extended from 1–5 to 0–10.	The scores may express a higher differentiation due to the smaller increments. Through the wider score range, inter-scorer consistency may decrease.
Algorithm	Wijeyamohan et al. (2014)	Asian elephant (*Elephas maximus*)	Addition of score 0 for extremely emaciated elephants. Thus the score range was extended from 1–10 to 0–10.	Higher differentiation for elephants in poor condition.
Overview	Fernando et al. (2009)	Asian elephant (*Elephas maximus*)	Combination of the exemplary pictures with the detailed description provided in Morfeld et al. (2014) and Wijeyamohan et al. (2014).	More assistance for unexperienced scorers which may lead to a higher intra- and inter-scorer consistency of the results.
Overview	Morfeld et al. (2014)	African elephant (*Loxodonta africana*)	Addition of score 0 for extremely emaciated elephants. Thus the score range was extended from 1–5 to 0–10. Combination of description with the one provided in Wijeyamohan et al. (2014).	Higher differentiation for elephants in poor condition.
Overview	Wijeyamohan et al. (2014)	Asian elephant (*Elephas maximus*)	Addition of score 0 for extremely emaciated elephants. Thus the score range was extended from 1–10 to 0–10. Combination of description with the one provided in Morfeld et al. (2014).	Higher differentiation for elephants in poor condition.

prominence. In comparison, the visibility of the backbone determines whether an elephant with unrecognisable ribs is given a BCS of 4 or 5.

Overview body condition scoring

Fernando et al. (2009), Morfeld et al. (2014) and Wijeyamohan et al. (2014) suggest systems basing on example photographs and corresponding descriptions for each score. Doing so, the typically assessed body areas are evaluated, but not scored individually. Thus, no defined prioritisation exists between them.

Neither Morfeld et al. (2014) nor Wijeyamohan et al. (2014) compare BCS obtained following a flow chart algorithm and BCS obtained by overview scoring. Scoring black rhinoceroses, Reuter and Adcock (1998) reported the best inter-observer repeatability when the scores given to the various body regions were combined. In contrast, Isensee et al. (2014) found in dairy cattle that results showed a stronger correlation to fat measurements if body regions were not scored individually, but a “general impression” overview scoring was applied. Obviously, the presentation of example scores together with a minimal description will be more practical under field conditions, due to its simplicity. Moreover, it requires less expertise from the evaluator, as intended especially by Fernando et al. (2009).

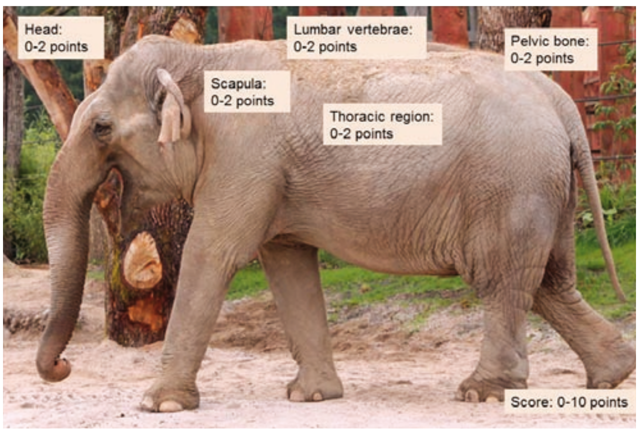

Figure 1. Composite body condition scoring in elephants modified according to Wemmer et al. (2006).

Testing the different approaches to visual BCS

Method

In order to demonstrate differences between the various visual scoring approaches, a set of 30 lateral photographs of 30 different individual European zoo elephants, 15 African (*Loxodonta africana*) and 15 Asian (*Elephas maximus*), was given to 18 individual veterinary students (3rd and 4th year students from the universities of Bern and Zurich) with no experience in elephant BCS scoring. The picture sets for both species were balanced regarding gender distribution, but not regarding score ranges. The latter was assumed to be practical with respect to the existing literature, where comparable protocols have been applied for Asian and African elephants (Morfeld et al. 2014, 2016). A self-explanatory instruction sheet for each scoring approach was supplied to the students together with the test documents. No further instructions were given. Each student scored all 30 elephants, 10 with the overview method (Fernando et al. 2009; Morfeld et al. 2014, Wijeyamohan et al. 2014), 10 with the composite method (Wemmer et al. 2006) and 10 with the algorithm method (Morfeld et al. 2014; Wijeyamohan et al. 2014), i.e. no student scored the same individual twice. The three scoring systems were modified so that all yielded the same number of scores (0–10). In doing so, we kept the number of modifications to a minimum (listed in Table 4). The modified protocols are depicted as they were used in the instruction sheet (Fig. 1–3). Under the assumption that there is no evidence for a difference in body fat deposition between elephant species, a single protocol was applied for Asian

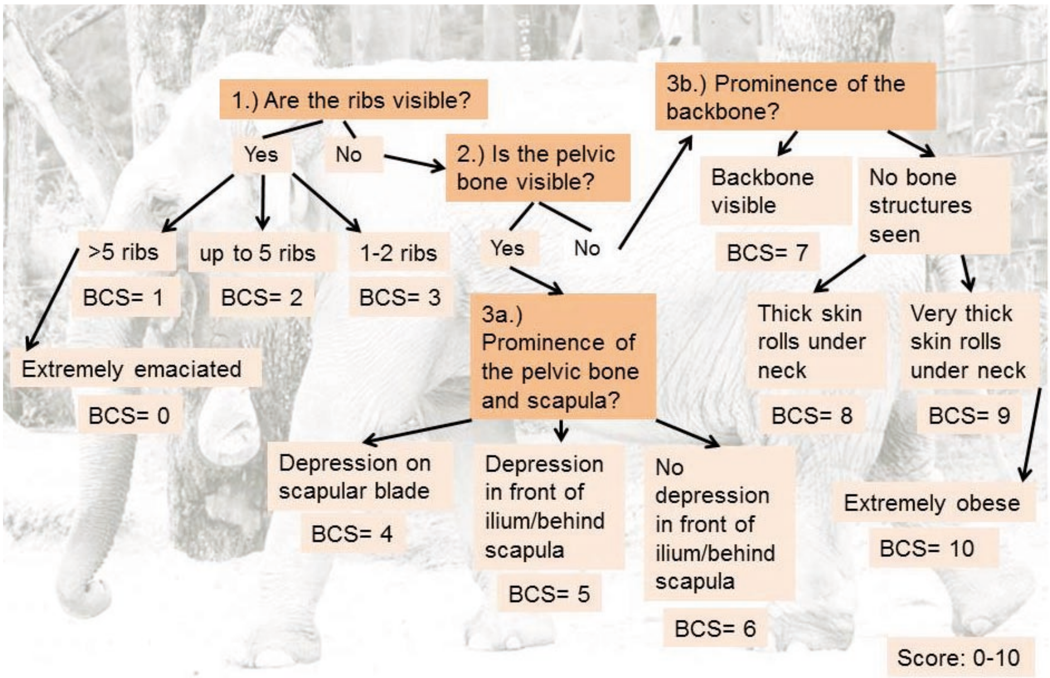

Figure 2. Algorithm body condition scoring in elephants modified according to Morfeld et al. (2014) and Wijeyamohan et al. (2014).

and African elephants. Test duration was limited to approximately 15 minutes per 10 photographs, with breaks of variable duration between the scoring sessions.

Differences between scoring methods were analysed with repeated measurements ANOVA (using the individual elephants as the basis of comparison, with the three methods the repeated measures for each animal) with a Sidak post hoc test. Additionally, for each scoring method, all 30 elephants were compared using ANOVA and Dunnet's T post hoc test (due to inequal variances), and the number of individual pairs with significant differences were counted (out of all 435 possible pairs). Finally, a General Linear Model (GLM) was performed with BCS as the dependent variable, student as a random factor, and both method and elephant species as fixed factors; normal distribution of residuals was confirmed by Kolgomorov–Smirnov test. The level of significance was set to 0.05.

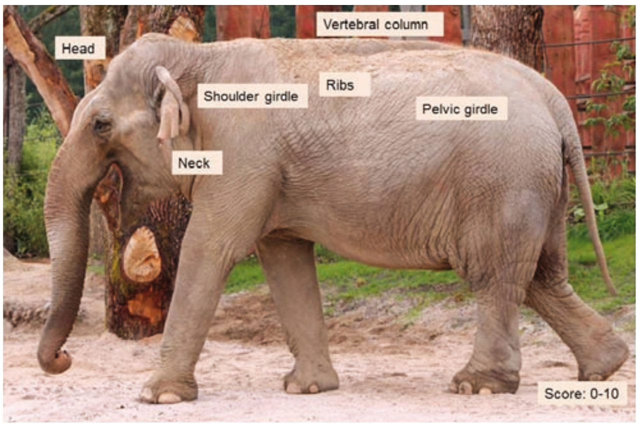

Figure 3. Overview body condition scoring in elephants modified according to Fernando et al. (2009), Morfeld et al. (2014) and Wijeyamohan et al. (2014).

Results

The algorithm method resulted in 26 significantly different pairs, the composite method in 55 significantly different pairs, and the overview method in 74 significantly different pairs. Across all individuals, composite scoring resulted in the largest range of mean and median BCS for individual animals (mean 2.7–9.5), followed by overview scoring (3.0–8.8), and algorithm scoring had the lowest range of scores (3.0–8.0) (Fig. 4). There was more inter-observer variation with the composite method (Table 5). Concerning the minimum score, a difference between the approaches was detectable, with composite scoring showing a significantly lower value than the other systems (Table 5). There were no significant differences in the overall mean, median and maximum scores between methods (Table 5). In the GLM, the random factor "student" was significant ($F_{20,606}$ = 2.405, P = 0.001), indicating systematic differences between the individual students; method was not significant ($F_{2,606}$ = 1.335, P = 0.264); and there was a significant difference between the two elephant species ($F_{1,606}$ = 116.821, P < 0.001, African: 5.2 ±1.8, range 1–10; vs Asian: 6.7 ±1.8, range 3–10), reflecting the fact that we had not aimed to balance BCS scores across species when selecting our example pictures.

Discussion

Our results show significantly higher inter-observer repeatability for the overview and algorithm approaches, while the composite protocol leads to more variability between scorers. A possible explanation for the decreased inter-observer repeatability of the composite approach might be the segmented mode of this system. While the other protocols consider the whole elephant, the composite method clearly subdivides the animal into separate regions. Reported results from a similar comparison in dairy cattle corroborate this hypothesis (Isensee et al. 2014). Moreover, the composite system weighs head and scapula equally with the remaining regions. In contrast, the algorithm and overview approach put the main emphasis on the lumbar region, the backbone and the

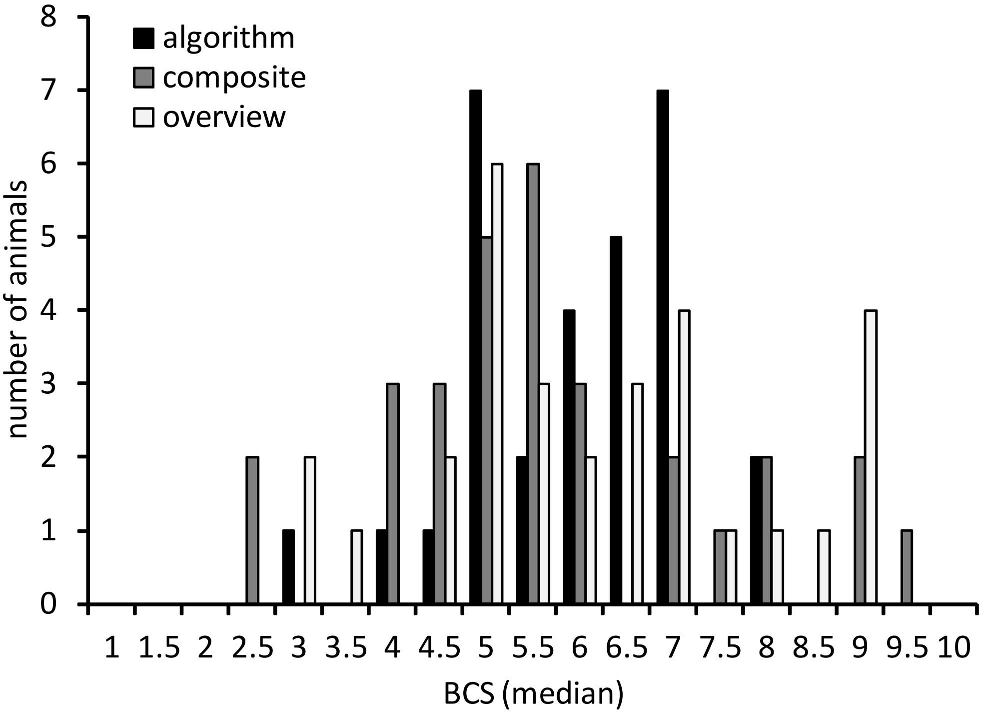

Figure 4. Differentiation of individual zoo elephant body condition scores (BCS) (median) by three different scoring approaches.

ribs, with minimal consideration of the head and shoulder areas. With respect to the most current species-specific publications, the former body regions can be assumed to be the critical ones for an elephant's condition (Morfeld et al. 2014, 2016). Our results are in contrast to those of Reuter and Adcock (1998), who reported the most repeatable mean scores for black rhinos by the composite method. This discrepancy might be caused by the inherent differences in the corresponding protocols. While we used a system modified from Wemmer et al. (2006), containing five body regions with three gradations in each, Reuter and Adcock (1998) scored seven body regions with five gradations each. This might have led to more reliable results in the rhino study. Thus, it can be speculated that the composite approach in elephants could be improved by extending the number of scored body regions and/or the number of increments. In doing so, the intended simplicity and practicability of a scoring system should not be forgotten.

Table 5. Mean (±SD) body condition scoring (BCS) means, medians, minima, maxima, and ranges for 30 zoo elephants scored by three different methods by six scorers per animal. Different superscripts (a, b) within a row indicate significant differences between the scoring methods.

	Overview	Composite	Algorithm	P-value (method)
Mean	6.1 ±1.6	5.2 ±1.7	5.9 ±1.1	0.208
Median	6.2 ±1.7	5.7 ±1.8	6.0 ±1.2	0.135
Minimum	4.6 ±1.7[a]	3.9 ±1.9[b]	4.5 ±1.1[ab]	0.020
Maximum	7.5 ±1.6	7.7 ±1.6	7.4 ±1.4	0.165
Range	2.8 ±1.0[a]	3.8 ±1.4[b]	2.9 ±1.0[a]	0.002

Whether our findings are representative for a variety of people (e.g. veterinarians, elephant handlers) and other animal species needs to be tested in further studies. Moreover, our investigation explicitly used the lateral view of an elephant. It is possible that the evaluation of various views could lead to differing results. The reported difference in minimum scores between the methods indicates an inconsistent application of the categories in elephants of reduced condition. For animals in reduced condition, overview and algorithm approaches provided a higher consistency in scores compared to the composite method. This finding may indicate that refined scoring criteria for individuals of low body condition should be emphasised in the development of future composite-based systems. The overall consistency of mean, median and maximum scores between methods may indicate that overall results may be comparable between studies, independent of the scoring approach applied. Additionally, the overall consistency of these results can be interpreted as confirmation of the practicability and reliability of the visual scoring approach in general. Based on our limited findings, the overview scoring approach can be recommended as a reliable method with a high level of differentiation in the evaluation of elephant body condition.

Practical impact of visual BCS on zoo animal husbandry

BCS have been found to correlate with various individual, environmental and husbandry-related factors (Table 3); such studies underline the usefulness of BCS.

One important question in applying BCS is at what intervals the scoring should be done.

The current literature provides few guidelines on this. In geese, Clausen et al. (2015) found that poor condition after harsh winters was detectable over a timeframe of at most two months. Investigating the diet of Asian and African elephants in Brazilian zoos, Carneiro et al. (2015) demonstrated visually observable effects on their body condition three months after dietary reduction. In their report on free-ranging African elephant bulls suffering from injuries, Ganswindt et al. (2010) recognised a decrease in their physical condition over two months. Thus, an interval of 2–3 months seems reasonable for body condition scoring in elephants. Smaller species should theoretically be scored more frequently due to their increased metabolism. In this respect, the 2–3 month interval for elephants should be considered the maximum time interval. This recommendation is assumed to be adequate for both Asian and African elephants; no evidence concerning their potentially different subcutaneous fat deposition has been reported yet. Morfeld et al. (2016) demonstrated the reliability of a comparable BCS system for the Asian as well as the African species.

In farm animals, efforts are directed towards including visual BCS systems in automated techniques for continuous animal status surveillance (Bewley et al. 2008; Azzaro et al. 2011; Bauer et al. 2012). In this process, strictly standardised photographs are required that facilitate the BCS evaluation by computer programs, thus reducing the method´s subjectivity and personnel effort (Ferguson et al. 2006; Bewley et al. 2008). Although no practically applicable automated systems are available yet, promising preliminary results have been reported (Negretti et al. 2008; Bauer et al. 2012; Bercovich et al. 2013). In zoo animal species with their significantly wider anatomical and morphological variability, such automated systems may be difficult to develop. However, using established BCS procedures on a regular basis with storage of standardised photographs, digital archives may be set up to allow monitoring individual body condition development over time. Digital photography could thus become part of an individual zoo animal's life history, completing health and reproductive records.

To conclude, visual body condition scoring systems can be considered a helpful tool in weight management of zoo animal species. This has been shown especially in rhinos and elephants, where weighing is often impractical. Regular standardised pictorial documentation of individuals with subsequent development of a corresponding digital archive is strongly recommended. This approach may provide zoos with a simple, practical and reliable monitoring tool for diet and husbandry concepts of their animals, including retrospective assessments. Regular BCS monitoring may also serve as an early warning system in health monitoring of wild and zoo animals. With respect to the results of the current study, scoring in elephants may be best completed using overview and/or algorithm methods.

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Body condition scores in European zoo elephants (*Elephas maximus* and *Loxodonta africana*) - status quo and influencing factors

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Body condition scores of European zoo elephants (*Elephas maximus* and *Loxodonta africana*): Status quo and influencing factors

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Abstract

Obesity is a common problem in captive elephants. Therefore, physical state monitoring presents a critical aspect in preventive elephant healthcare. Some institutions lack the equipment to weigh elephants regularly, so body condition scoring (BCS) is a valuable alternative tool. As yet, the BCS of both elephant species has not been assessed comprehensively for the European captive population. Using a previously validated visual BCS protocol, we assessed 192 African (*Loxodonta africana*) and 326 Asian elephants (*Elephas maximus*) living in European zoos (97% of the living European elephant population). The majority of elephants scored in the upper categories with 56% of adults assessed in the range 7–10 out of 10. Adult Asian elephants had significantly lower BCS (males: mean 6.2 ± 1.0, median 6.0, range 4–8; females: mean 6.6 ± 1.3, median 6.0, range 3–9) than African elephants (males: mean 6.7 ± 0.7, median 6.0, range 6–8; females: mean 6.9 ± 1.2, median 6.0, range 1–9). Comparison with samples of free-ranging populations (163 Asian elephants and 121 African elephants) revealed significantly lower scores in free-ranging elephants independent of species, age and sex category. Compared to previous reports from captive populations, the European zoo elephant population is nevertheless less obese. In adult Asian elephant females, BCS was significantly correlated to their breeding status with lower scores in current breeders; however, breeding status was also correlated to group size, enclosure size, and a diet with less vegetables. Further attention to zoo elephant weight management is recommended with regular longitudinal monitoring by body condition scoring.

Introduction

Because of their body size, intelligence, importance to the public and conservation status, captive management of African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) is challenging. Optimising nutritional intake for elephants in captivity can be problematic, and several reports have highlighted the problems of feeding regimes and found obesity to be common (Harris et al. 2008; Hatt and Clauss 2006; Morfeld et al. 2016). Weight management is therefore an important focus for good elephant husbandry, and body weight monitoring an important part of preventative medicine. However, the sheer size and expense of the required technical equipment means regular weight monitoring might not be feasible for many elephant-keeping zoos. Visual body condition scoring (BCS) is considered a useful method to reliably assess zoo animals including elephants (reviewed in Schiffmann et al. 2017), although none of these have defined an ideal score range with regards to health.

Several indices have recently been developed for elephants and applied in free-ranging as well as semi-captive and captive populations (Fernando et al. 2009; Morfeld et al. 2014; Morfeld et al. 2016; Treiber et al. 2012; Wemmer et al. 2006; Wijeyamohan et al. 2015). Scores are affected by age (Chusyd et al. 2018; Somgird et al. 2016b), sex (Godagama et al. 1998; Morfeld et al. 2016; Pinter-Wollman et al. 2009; Ramesh et al. 2011), living conditions (Morfeld et al. 2014; Wijeyamohan et al. 2015), season (Albl 1971; De Klerk 2009; Foley et al. 2001; Pinter-Wollman et al. 2009; Pokharel et al. 2017; Ramesh et al. 2011; Ranjeewa et al. 2018), husbandry parameters (Harris et al. 2008; Morfeld et al. 2016), reproductive status such as lactation (De Klerk 2009), faecal glucocorticoid metabolites (Pokharel et al. 2017), history of translocation (Pinter-Wollman et al. 2009) and duration of musth (Poole 1989; Somgird et al. 2016b). More extended information on previous research on elephant body condition scoring is compiled in Supplement 1 (Table S1 and S2).

In general, values in the middle range of an index are considered ideal with reference to the protocols in pets and farm animals (Santarossa et al. 2017). Based on these assumptions, a high percentage of zoo elephants in the UK and North America have been evaluated as overweight or obese (Harris et al. 2008; Morfeld et al. 2016). Morfeld et al. (2016) conducted an extensive review of the North American zoo elephant population (240 elephants in 65 institutions). However, apart from Harris´ (2008) welfare evaluation of the entire UK zoo elephant population (n=70), no study has applied a BCS index to a substantial sample size in European captive elephants, which consists of about 500 individuals (Schwammer and Fruehwirth 2015; van Wees and Damen 2016). The aim of the present study was to establish a population-wide overview of elephant body condition in these 500 animals and to perform a comparison to two free-ranging populations.

Material and methods

In January 2016, 189 African and 294 Asian elephants were included in the European endangered species program (EEP) studbooks for the European zoo elephant population. The studbook for the Asian species provides a list of 51 elephants that do not participate in the EEP. A corresponding list does not exist for the African elephant, although several individuals not recorded in the EEP are known to live in European zoos, resulting in a total of 534 individual elephants considered in our study.

Life history and husbandry data collection

Basic life history data of the individual elephants were taken from the current compilations in the EEP-studbooks at the end of March 2017 with subsequent data analysis until November 2017. Additionally, information concerning management system, enclosure sizes, diet composition, feeding regime, weight documentation and reproductive status were collected by interviewing staff members (veterinarians, curators and keepers) during visits on site or by questionnaire via mail or phone.

Body condition scoring

We used one standardised photograph showing the elephant in side profile as basis for the scoring, as for other recent scoring protocols (Fernando et al. 2009; Morfeld et al. 2014; Morfeld et al. 2016; Wijeyamohan et al. 2015). Pictures of European zoo elephants were taken while visiting facilities on site, and facilities

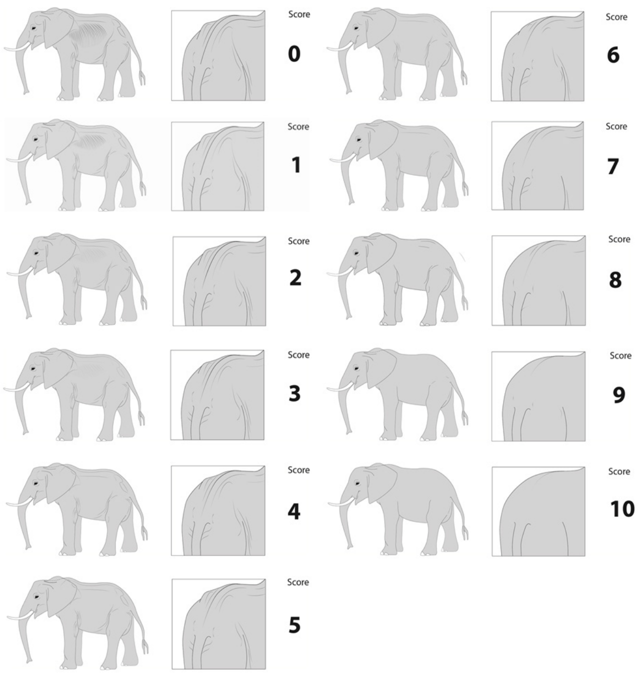

Figure 1. Example drawings used for body condition scoring of African elephants (Loxodonta africana) (drawings by Jeanne Peter)

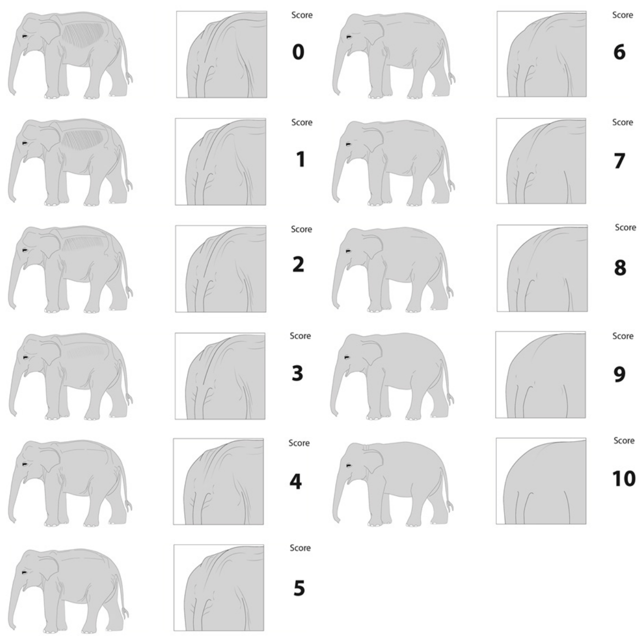

Figure 2. Example drawings used for body condition scoring of Asian elephants (Elephas maximus) (drawings by Jeanne Peter)

in which a personal visit was not feasible were contacted by mail or phone and asked to provide current photographs of their individual elephants. To be included in the study, a pictorial document had to fulfill the following criteria: i) datable to a month (where an accurate date was missing, the 1st day of the month was recorded); ii) clearly identifiable individual; iii) sufficient recognition of the relevant body regions (backbone, pelvic bone, ribs, skin fold on the base of the tail); iv) standing or moderate walking body position to allow reliable assessment; and v) adequate resolution of the photograph, based on recognition of the generic wrinkles on the skin surface of the elephant, absence of distinct patterns of shade or large amounts of hay, straw or other substrates on the back of the elephant.

To assign a consistent BCS to every photograph we combined species-specific indices in an overview following Schiffmann et al. (2017) (for African elephants from Morfeld et al. 2014; for Asian elephants from Fernando et al. 2009, Wijeyamohan et al. 2015 and Morfeld et al. 2016). Recent work has suggested scoring may reach a higher reproducibility and repeatability by using example drawings as opposed to pictures (Vieira et al. 2015). Therefore, we had exemplar drawings made for every score and each species that showed elephants in side profile and from behind (Figures 1 and 2). The focus was laid on the visibility of indicated bone structures of the lumbar region, which have been shown to correlate best with the amount of body fat in elephants (Albl 1971; Morfeld et al. 2014; Morfeld et al. 2016). In addition, the overall appearance of the elephant was taken into account and was considered more important than single characteristics (e.g. visibility of ribs or edges of the scapula), following the findings of Schiffmann et al. (2017). Elephant pictures were scored independently of age and sex by the first author, using the technical size of the picture to generate a random order to reduce observer bias. To check the method for intra-examiner agreement, a random sample (n=500) of pictures was evaluated twice and scores compared.

Collection of pictorial samples from free-ranging populations

We collected a sample of photographs from both species from the wild. For the Asian elephant, 163 photographs of the Yala National Park (Sri Lanka; 6° 16´N, 81° 20´ E) population taken randomly between 2006 and 2014 were scored. The individually pictured elephants were grouped into the following age and sex categories: calves (<5 years), juveniles (5–15 years), adult females (>15 years) and adult males (>15 years). We defined the applied categories on various age class systems for both elephant species (Arivazhagan and Sukumar 2008; Moss 2001; Pokharel et al. 2017). This sample consisted of 51 calves, 32 juveniles, 50 adult females and 30 adult males. For the African species, 121 photographs of the Amboseli National Park (Kenya; 2° 38´S, 37° 14´ E) population taken randomly between 2001 and 2016 were scored. This sample consisted of 29 calves, 28 juveniles, 40 adult females and 27 adult males. Both samples were balanced regarding age and sex category. We were unable to assess season for either free-ranging population, although seasonal changes in body condition do occur (De Klerk 2009; Foley et al. 2001; Ramesh et al. 2011; Ranjeewa et al. 2018).

Table 1. Body condition scores of the African elephant (*Loxodonta africana*) population in European zoos and a sample of their free-ranging counterparts in Amboseli National Park, Kenya

Age/sex category	N	Score range	Average ±SD	Median	First quartile	Third quartile
Calves (<5 years)**						
Zoo	12	6–8	7.15±0.69	7.00	7.00	8.00
free-ranging	29	5–8	6.39±0.79	6.00	6.00	7.00
Juveniles (5–15 years)**						
Zoo	48	5–8	6.45±0.71	6.00	6.00	7.00
free-ranging	28	5–8	5.89±0.74	6.00	5.00	6.00
Adult females (>15 years)***						
Zoo	108	1–9	6.90±1.19	7.00	6.00	8.00
free-ranging	40	5–8	6.03±0.85	6.00	5.00	6.75
Adult males (>15 years)(*)						
Zoo	21	6–8	6.67±0.75	7.00	6.00	7.00
free-ranging	27	5–8	6.33±0.83	6.00	6.00	7.00

Significant difference (U-test): *** P<0.001, ** P<0.01, * P<0.05; (*): P=0.054

Table 2. Body condition scores of the Asian elephant (*Elephas maximus*) population in European zoos and a sample of their free-ranging counterparts in Yala National Park, Sri Lanka

Age/sex category	N	Score range	Average ±SD	Median	First quartile	Third quartile
Calves (<5 years)***						
Zoo	49	4–9	6.59±0.98	7.00	6.00	7.00
free-ranging	51	3–7	5.39±0.92	5.00	5.00	6.00
Juveniles (5–15 years)***						
Zoo	69	5–9	6.72±1.16	7.00	6.00	7.00
free-ranging	32	3–7	5.25±0.89	5.00	4.75	6.00
Adult females (>15 years)***						
Zoo	179	3–9	6.58±1.29	7.00	6.00	7.00
free-ranging	50	3–7	5.30±1.02	5.00	5.00	6.00
Adult males (>15 years)*						
Zoo	29	4–8	6.21±0.98	6.00	6.00	7.00
free-ranging	30	2–7	5.53±1.04	6.00	5.00	6.00

Significant difference (U-test): *** P<0.001, ** P<0.01, * P<0.05

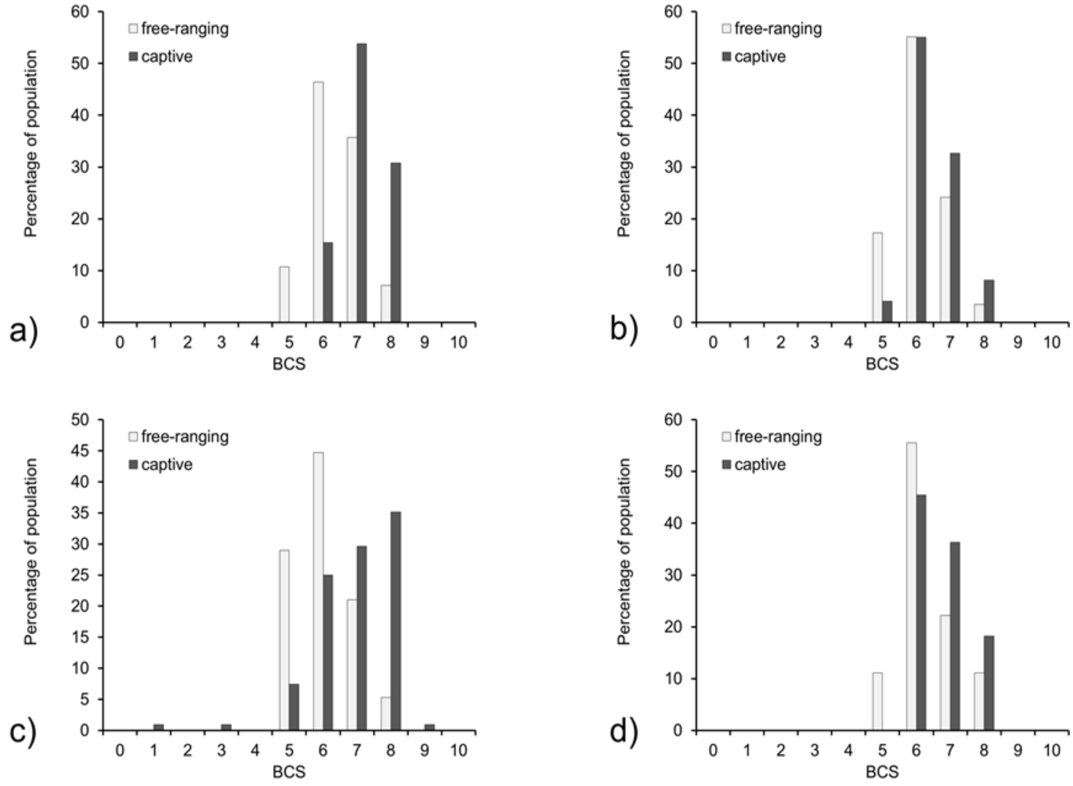

Figure 3. Distribution of body condition scores in populations of free-ranging (n=121) and captive (n=189) African elephants (*Loxodonta africana*). a) Calves (<5 years), b) Juveniles (5–15 years), c) Adult females (>15 years), d) Adult males (>15 years)

Comparison with literature data

Due to the differences in the BCS systems used in the literature, absolute scores were not directly comparable: for example, in a system with a score range of 1–5, a BCS of 5 indicates obesity, whereas it would indicate an intermediate state in a system with a score range from 1–10. In order to put our results into a comparative perspective, we compared our data (BCS range 0–10) to the data of Morfeld et al. (2016) (BCS range 1–5), equating our scores of 9–10 to their score of 5, our scores of 7–8 to their score of 4, etc. Additionally, we calculated a standardised score by expressing the mean or median score reported in publications as a proportion of the total score range, adjusting the range so that higher values indicate obesity. Thus, for example, a standardised score of 0.8 would indicate that the mean/median score was in the last (upper) quartile of the score range.

Statistical analysis

Body condition scores are non-parametric data by definition, and therefore, data should be represented by medians and quartiles; however, following recent convention (Chusyd et al. 2018; De Klerk 2009; Foley et al. 2001; Godagama et al. 1998; Harris et al. 2008; Kumar et al. 2014; Morfeld and Brown 2016; Morfeld et al. 2014; Morfeld et al. 2016; Ranjeewa et al. 2018; Somgird et al. 2016b; Wemmer et al. 2006), we additionally report means and standard deviations. To compare BCS of different groups, the Mann-Whitney U test was used. Correlations with quantitative measures were assessed by Spearman's correlation coefficient. This was done for the following parameters: age [years], group size [number of elephants sharing area], amount [all diet amounts are in estimated dry matter] concentrate fed [kg/day], amount bread fed [kg/day], amount fruit fed [kg/day], amount vegetables fed [kg/day], total amount fed (excluding roughage) [kg/day], feeding frequency [feedings/day], feeding enrichment [amount of different devices], amount training [minutes/day], enclosure area indoors [m2], outdoors [m2] and total enclosure area [m2]. More comprehensive evaluation was only performed in Asian elephant females, in which a variety of individual factors were correlated with the BCS; in this case, non-parametric correlations between the significant factors were analysed, and a General Linear Model was performed using ranked data. Statistical procedures were performed in SPSS 23.0.0 (IBM Corp., Armonk, NY), with the significance level set to 0.05.

Results

Collection of pictorial documents

In total, 64 different facilities maintaining 140 African and 228 Asian elephants were visited (all by CS), and elephants were photographed on site between beginning of January 2016 and the end of March 2017. Together with photographs received by

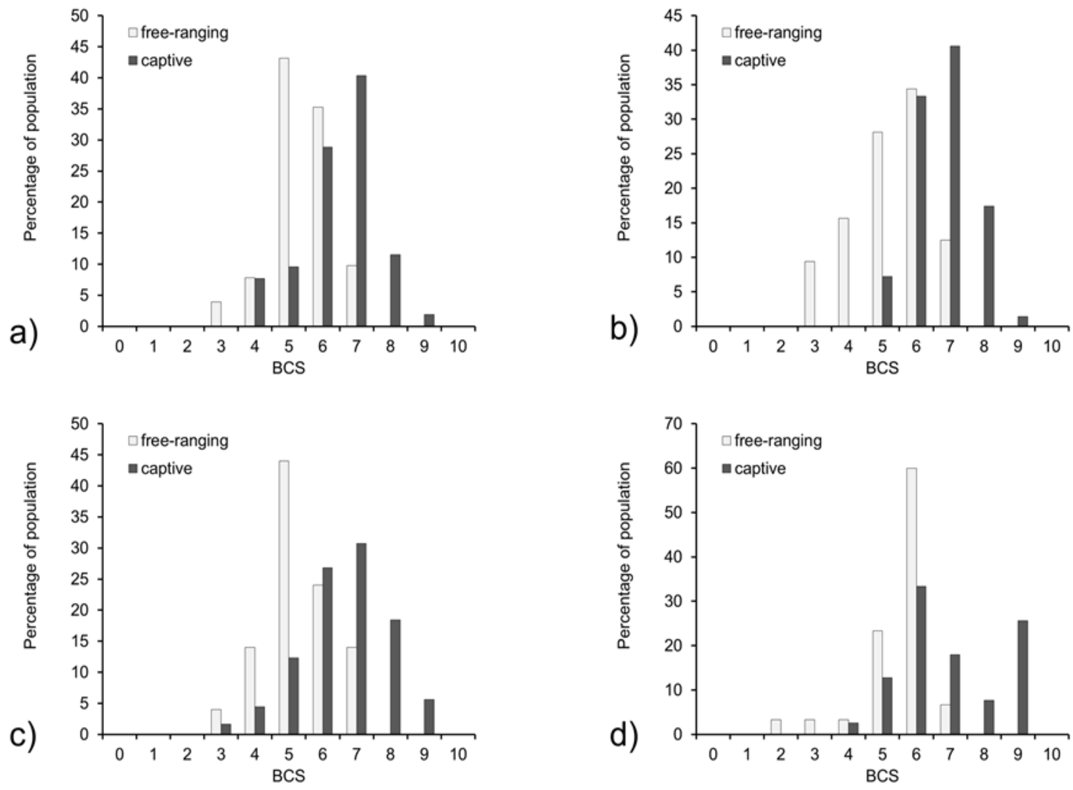

Figure 4. Distribution of body condition scores in populations of free-ranging (n=163) and captive (n=326) Asian elephants (*Elephas maximus*). a) Calves (<5 years), b) Juveniles (5–15 years), c) Adult females (>15 years), d) Adult males (>15 years)

mail, 192 African and 326 Asian elephants of European zoos were included in this study. This sample consisted mainly of elephants participating in the EEP´s (470/518; 91%), but elephants of non-member facilities (48/518; 9%) were included as well.

Life history data collection

Documentation and availability of life history and husbandry data varied considerably between institutions. As expected, comprehensive husbandry data were received only during on-site visits. Forty of the 64 visited facilities had a scale to weigh their elephants, and 35 of them conducted weight monitoring on a regular basis. Seven institutions had established body-condition scoring protocols, but only four of these zoos documented body scores with photos. While some facilities applied individual diet sheets for each elephant, others did not have any written document at all and it was up to the keepers how much of which ingredient was fed. Most institutions had some guidelines, which could be adapted by the keepers. Females were monitored much more closely for reproductive status than males, and most facilities used hormonal monitoring via urine or fecal testing. Only two institutions were found to accurately document musth behavior in their males. Investigation of potential correlation patterns between BCS and specific pathologies was not possible due to the diversity in the extent of available medical records.

Data analysis and check for repeatability

The intra-observer agreement generated identical scores in 366 cases (366/500; 73.2%) and a variance by 1 score in 132 cases (132/500; 26.4%). Thus, the repeatability in the range of maximally 1 scoring point was given in 99.6% of the pictures, which was considered acceptable for a protocol with a scoring range from 0 to 10.

Statistical analysis

Body condition scores, their distribution for the European zoo elephant population as well as both free-ranging samples are compiled in Tables 1 and 2 and Figures 3 and 4. Compared to their free-ranging counterparts, elephants kept in European zoos showed significantly higher scores (P<0.05). This was valid for all sex and age categories with the exception of adult African elephant males, in which the difference was marginally below the level of significance (P=0.054).

Within the captive population, there were significant species differences for all age classes; males (Asian mean: 6.21±0.98, median: 6.00, range: 4–8 vs. African mean: 6.77±0.75, median: 7.00, range: 6–7; P=0.032), females (Asian mean: 6.58±1.29, median: 7.00, range: 3–9 vs. African mean: 6.88±1.19, median: 7.00, range 1–9; P=0.024), calves (Asian mean: 6.59±0.98, median: 7.00, range: 4–9 vs. African mean: 7.15±0.69, median: 7.00, range 6–8; P=0.045), but not for juveniles (Asian mean: 6.73±0.89,

Table 3. Nonparametric correlation of husbandry parameters with body condition in African elephants (*Loxodonta africana*) kept in European zoos

Parameter tested	Calves (<5 years)	Juveniles (5–15 years)	Adult females (>15 years)	Adult males (>15 years)
Age [years]	R=0.14 ; P=0.660; n=13	R=-0.10; P=0.487; n=49	R=-0.00; P=0.968; n=108	R=0.19; P=0.410; n=22
Group size [n elephants sharing area]	n.a.	R=-0.09; P=0.715; n=20	R=-0.16; P=0.104; n=108	n.a.
Amount concentrate [kg*day]	n.a.	R=-0.12; P=0.535; n=31	R=0.12; P=0.389; n=58	R=0.22; P=0.443 n=14
Amount bread [kg*/day]	n.a.	R=-0.18; P=0.339; n=31	R=-0.27; P=0.042; n=58	R=-0.16; P=0.593; n=14
Amount fruit [kg*/day]	n.a.	R=0.34; P=0.061; n=32	R=-0.02; P=0.899; n=58	R=0.33; P=0.250; n=14
Amount vegetables [kg*/day]	n.a.	R=0.21; P=0.255; n=32	R=0.13; P=0.334; n=58	R=0.10; P=0.733; n=14
Total amount diet (excluding roughage) [kg*/day]	n.a.	R=-0.01; P=0.956; n=32	R=0.12; P=0.382; n=58	R=0.17; P=0.574; n=14
Feeding frequency [feedings/day]	n.a.	R=-0.23; P=0.258; n=27	R=-0.26; P=0.051; n=56	R=-0.35; P=0.266; n=12
Feeding enrichment [amount of different devices]	n.a.	R=0.03; P=0.874; n=32	R=-0.20; P=0.117; n=64	R=-0.57; P=0.034; n=14
Amount training [minutes/day]	n.a.	R=-0.25; P=0.188; n=30	R=-0.06; P=0.632; n=61	R=0.34; P=0.250; n=13
Enclosure area indoors [m2]	n.a.	R=0.45; P=0.041; n=21	R=-0.10; P=0.453; n=61	R=-0.13; P=0.697; n=11
Enclosure area outdoors [m2]	n.a.	R=0.13; P=0.477; n=33	R=0.02; P=0.891; n=73	R=-0.19; P=0.502; n=15
Total enclosure area [m2]	n.a.	R=0.20; P=0.405; n=20	R=0.03; P=0.841; n=57	R=-0.16; P=0.635; n=11

n.a.=not analyzed (n too low); in bold: significant correlations (P<0.05); * estimated dry matter

Table 4. Nonparametric correlation of husbandry parameters with body condition in Asian elephants (*Elephas maximus*) kept in European zoos

Parameter tested	Calves (<5 years)	Juveniles (5–15 years)	Adult females (>15 years)	Adult males (>15 years)
Age [years]	R=0.32; P=0.024; n=49	R=-0.22; P=0.073; n=69	R=0.09; P=0.258; n=179	R=-0.19; P=0.318; n=29
Group size [n elephants sharing area]	n.a.	R=-0.56; P=0.002; n=28	R=-0.22; P=0.003; n=179	n.a.
Amount concentrate [kg*/day]	R=-0.12; P=0.649; n=17	R=0.01; P=0.915; n=63	R=0.08; P=0.337; n=135	R=0.15; P=0.495; n=23
Amount bread [kg*/day]	R=0.11; P=0.674; n=17	R=0.06; P=0.629; n =63	R=-0.06; P=0.491; n=140	R=-0.07; P=0.754; n=24
Amount fruit [kg*/day]	R=0.29; P=0.259; n=17	R=0.386; P=0.002; n=63	R=0.10; P=0.239; n=139	R=0.44; P=0.032; n=24
Amount vegetables [kg*/day]	R=-0.11; P=0.672; n=17	R=0.07; P=0.623; n=60	R=0.20; P=0.018; n=139	R=0.47; P=0.023; n=23
Total amount diet (excluding roughage) [kg*/day]	R=0.04; P=0.871; n=17	R=0.09; P=0.489; n=63	R=0.07; P=0.428; n=141	R=0.32; P=0.122; n=24
Feeding frequency [feedings/day]	R=0.52; P=0.029; n=18	R=0.28; P=0.058; n=48	R=0.03; P=0.771; n=78	R=0.36; P=0.166; n=16
Feeding enrichment [amount of different devices]	R=0.31; P=0.177; n=21	R=0.34; P=0.018; n=49	R=-0.05; P=0.587; n=102	R=-0.17; P=0.492; n=19
Amount training [minutes/day]	R=-0.17; P=0.467; n=20	R=0.05; P=0.762; n=43	R=-0.12; P=0.255; n=93	R=0.37; P=0.136; n=18
Enclosure area indoors [m2]	R=0.08; P=0.742; n=21	R=0.05; P=0.679; n=62	R=-0.24; P=0.002; n=161	R=-0.24; P=0.243; n=26
Enclosure area outdoors [m2]	R=-0.11; P=0.620; n=23	R=-0.18; P=0.155; n=67	R=-0.23; P=0.003; n=165	R=0.01; P=0.955; n=28
Total enclosure area [m2]	R=-0.12; P=0.603; n=22	R=-0.13; P=0.317; n=62	R=-0.27; P=0.001; n=161	R=-0.02; P=0.949; n=26

in bold: significant correlations (P < 0.05); *:estimated dry matter

median: 7.00, range: 5–9 vs. African mean: 6.45±0.71, median: 6.00, range 5–8; P=0.061). Within species, there was no significant difference in BCS according to management system or the origin of elephants (wild caught vs. captive born) for any of the species/age groups. There were no significant differences between male and female adults within either species (data not shown). In neither species did scores differ between females that were cycling, pregnant, lactating or non-cycling. Additionally, we found no correlation between lactation status and BCS (data not shown). Breeding and non-breeding males of either species did not differ in BCS. However, in Asian adult females, currently breeding females (defined as having at least one offspring during the past 5 years or being currently pregnant) had significantly lower BCS (n=44, mean: 6.18±1.33, median: 6.00, range 3–9) than non-breeding females (n=108, mean: 6.71±1.25, median: 7.00, range 3–9; P=0.021). No such difference was observed in African females

Table 5. Comparison of body condition score distribution in recent population-wide assessments of North American and European zoo elephants

	Morfeld et al. (2016) North American population (mean age: 31.1 ± 13.7 years)						Present study European population (mean age: 34.9 ± 11.3 years)				
	African elephant (n=132)		Asian elephant (n=108)		Total		African elephant (n=130)		Asian elephant (n=218)		Total
Scoring range: 1-5	Female n=106	Male n=26	Female n=85	Male n=23	n=240	Scoring range: 0-10	Female n=108	Male n=22	Female n=179	Male n=39	n=348
Score	Percentage					Score	Percentage				
1	0	0	2.3	0	0.8	0-2	0.9	0	0	0	0.3
2	0	3.8	5.9	8.7	3.3	3-4	0.9	0	6.1	2.6	3.7
3	21.7	38.5	16.5	26.1	22.1	5-6	32.4	45.5	39.1	46.2	38.2
4	45.3	50.0	27.1	47.8	39.6	7-8	64.8	54.5	49.1	25.6	51.7
5	33.0	7.7	48.2	17.4	34.2	9-10	0.9	0	5.6	25.6	6.0

(P=0.619). Similarly, adult Asian females living in a breeding group had significantly lower BCS (n=98, mean: 6.39±1.31, median: 6.00, range: 3–9; P=0.022) than those not living in a breeding group (n=81, mean: 6.82±1.25, median: 7.00, range 4–9). Again, no such difference was evident in African females (P=0.941), or juveniles of either species. There were neither significant differences between non-breeders and previous breeders, nor between current and previous breeders, and there was no significant difference in any group depending on whether animals were weighed or BCS was applied regularly or not (data not shown). Results of non-parametric correlation tests between BCS and husbandry parameters are presented in Tables 3 and 4. For the African species, BCS in juveniles was positively correlated with indoor area, while for adult females and males, there was a significant

Table 6. Overview of research conducted on body condition scoring in African elephants (*Loxodonta africana*)

Living conditions	n	Investigated sex/age categories [years] ± SD	Standardized average score (average score/scoring range)	Correlating Parameters	Reference
free-ranging	240	all ages of both sexes	-	season	Albl (1971)
free-ranging	22	adult males only	-	stage of musth	Poole (1989)
free-ranging	not indicated	reproductively active females only	0.56-0.80 (mean)	season	Foley et al. (2001)
free-ranging	4-107 (depending on season and category)	all age classes females only	0.40-0.70 (mean)	season, nutritional resources, lactation	De Klerk (2009)
free-ranging	544	adults only	-	season, sex, history of translocation	Pinter-Wollman et al. (2009)
free-ranging	57	females only (10-45 years)	0.60 (median)	-	Morfeld et al. (2014)
free-ranging	124	all age classes of both sexes	0.56 (mean); 0.55 (median)	-	this study
semi-captive$_a$	7	juveniles of both sexes ; 10.7 ± 2.8	0.83 (mean and median)	-	Velthuizen (2008)
captive$_b$	not indicated	all age classes of both sexes	0.60 (mean)	handling method	Harris et al. (2008)
captive$_c$	50	females only (10-45 years)	0.80 (median)	captivity	Morfeld et al. (2014)
captive$_c$	132	both sexes, age not separately indicated for species	0.80 (mean and median)	sex, walking exercise, feeding schedule & methods	Morfeld et al. (2016)
captive$_c$	20	females; 34.75 ± 8.17	0.77 (mean); 0.80 (median)	age, body mass, fat mass	Chusyd et al. (2018)
captive$_d$	189	adults of both sexes; 30.7 ± 8.4	0.62 (mean); 0.64 (median)	-	this study

captive: investigated animals live in captivity; semi-captive: investigated animals live in semi-captive conditions in countries of origin; free-ranging: free-ranging individuals were investigated, a: elephant training facility in South Africa; b: UK zoos; c: North American zoos; d: European zoos

Table 7. Overview of research conducted on body condition scoring in Asian elephants (*Elephas maximus*)

Living conditions	n	Investigated sex/age categories; mean age [years] ± SD	Standardized average score (average score/scoring range)	Correlating parameters	Reference
free-ranging	-	not indicated	-	-	Fernando et al. (2009)
free-ranging	653	calves, juveniles, sub-adults and adults of both sexes	-	season, faecal glucocorticoid metabolites	Pokharel et al. (2017)
free-ranging	1622	calves, juveniles, sub-adults and adults of both sexes	-	season, sex	Ramesh et al. (2011)
free-ranging	27	not indicated	0.60 (median and mean)	-	Wijeyamohan et al. (2015)
free-ranging	3175 (containing 526 individuals at different times)	adult females, sub-adult and adult males	0.51 (mean)	reservoir water level, sex, age-size class in males	Ranjeewa et al. (2018)
free-ranging	163	all age classes of both sexes	0.49 (mean); 0.45 (median)	-	this study
semi-captive$_a$	119	All age classes of both sexes; age known for 50 elephants: 17.5 ± 1.8	0.61 (mean)	-	Wemmer et al. (2006)
semi-captive$_b$	42	all age classes of both sexes; 20.6 ± 17.7	0.35 (mean)	-	Harris et al. (2008)
semi-captive$_c$	22	mature females only; 29.4 ± 9.9)	0.73 (mean and median)	-	Thitaram et al. (2008)
semi-captive$_c$	5	adult males only; 41.4 ± 13.1	0.63 (mean); 0.75 (median)	-	Somgird et al. (2016a)
semi-captive$_d$	9	adult males only; 58.4 ± 8.6	0.69 (mean); 0.75 (median)	age, duration of musth Phase	Somgird et al. (2016b)
captive$_e$	140	all age classes of both sexes; 37.4 ± 1.4	0.58 (mean and median)	sex	Godagama et al. (1998)
captive$_f$	not indicated	all age classes of both sexes	0.58 (mean)	handling method	Harris et al. (2008)
captive$_g$	12	not indicated	0.69 (median)	rump fat thickness	Treiber et al. (2012)
captive$_h$	12	adults and juveniles of both sexes; 34.0 ± 15.6	0.60 (mean); 0.68 (median)		Kumar et al. (2014)
captive$_i$	10	adult and juvenile females of both sexes; 37 ± 19.93	0.57 (mean); 0.55 (median)	-	Romain et al. (2014)
captive$_g$	31	not indicated	0.80 (mean and median)	captivity	Wijeyamohan et al. (2015)
captive$_g$	108	both sexes, age not separately indicated for species	0.81 (mean); 0.8 (median)	sex, walking exercise, feeding schedule and methods	Morfeld et al. (2016)
captive$_j$	326	adults of both sexes; 37.6 ± 12.0	0.60 (mean); 0.64 (median)	captivity, breeding state, diet, enclosure size	this study

negative correlation of BCS with the amount of bread in the diet and the amount of feeding enrichment provided, respectively. In the Asian species, BCS in calves was positively correlated with age and feeding frequency. Juveniles and adult males showed both a positive correlation between BCS and amount of fruit in the diet, which also occurred for the amount of vegetables in the diet of adult females and males. Body condition scores in adult females were negatively correlated with the size of indoor, outdoor and total area.

Focusing on the various individual factors yielding a significant association with BCS in Asian females, group size was negatively correlated with the amount of vegetables fed ($R=-0.50$, $P<0.001$, $n=139$), and positively with living in a breeding group ($R=0.79$, $P<0.001$, $n=179$), being a breeder ($R=0.38$, $P<0.001$, $n=179$), and total enclosure area ($R=0.23$, $P=0.002$, $n=179$). Similarly, the total enclosure area was negatively correlated with the amount of vegetables fed ($R=-0.29$, $P=0.001$, $n=136$), positively with living in a breeding group ($R=0.51$, $P<0.001$, $n=161$) and positively with

Figure 5. Challenges encountered while scoring zoo elephant´s body condition: a) extraordinary hairiness, b) excessive hyperkeratosis, c) voluminous belly and d) well developed musculature

being a breeder (R=0.28, P<0.001, n=161). Using ranked data for BCS, the amount of vegetables fed and total enclosure area, a General Linear Model with BCS as dependent variable, group size, vegetables and area as covariates and living in a breeding group as a cofactor yielded a significant association with (ranked) total enclosure area only (F=11.320, P=0.001), whereas neither group size (F=0.187, P=0.666), the amount of vegetables fed (F=2.636, P=0.107) nor living in a breeding group (F=0.216, P=0.643) were significant.

Discussion

Reflection of our method

Data collection on site resulted in more comprehensive data especially concerning diet composition and management system than data collection via mail contact. Pictures of elephants taken by the author fulfilled the criteria to be included in 100% of the cases, whilst nearly 3.5% (5/150) of elephants for which pictures were received remotely did not pass this selection and were excluded from the study. Thus, elephants living in visited zoos might be overrepresented in our analysis. Ideally each elephant-keeping facility across Europe should have been visited, which was not feasible due to temporal and financial limitations. With respect to the data on the diets, it needs to be noted that amounts were based on the facilities' estimates of the amounts fed and not on actually measured intake data.

It can be questioned whether visual body condition scoring allows a reliable assessment of an elephant´s fat storage, because this method cannot consider intraabdominal adipose deposits. A recent study in horses detected a strong positive correlation between BCS and retroperitoneal fat score whilst no association between BCS and mesenteric or epicardial fat was found (Morrison et al. 2017). Whether this assumption is valid for elephants, too, will be hard to prove due to the lack of a method that allows assessment of intraabdominal fat deposits in a non-invasive way.

Although recommended as a management tool (Ward et al. 1999) and confirmed as viable by studies conducted in various species including elephants (Joblon et al. 2014; Morfeld et al. 2014; Morfeld et al. 2016; Pérez-Flores et al. 2016; Pettis et al. 2004; Pokharel et al. 2017; Wijeyamohan et al. 2015), BCS based on photographs has several limitations. First of all, standardisation regarding light conditions, ground planarity, movement and angle of the camera can be reached only to a certain extent. This limitation has been reported in cattle (Bewley et al. 2008) and might be even more pronounced in our work with respect to the significant variability between elephant-keeping facilities.

In order to reach the highest standardisation possible, the formulation of several criteria, which a photograph had to fulfill to be included in the study together with a strict selection process, were of paramount importance. During the scoring process two unexpected cases occurred, which led to the exclusion of further photographs. These were extraordinary hairiness and excessive hyperkeratosis in the lumbar region, prohibiting reliable scoring (Figures 5a and b).

Compared to the generally accepted protocol by Wemmer et al. (2006), our method focused on fewer body regions. However, these areas correlate strongest with subcutaneous measurements respectively serum triglyceride levels as indicators of fat storage in elephants (Albl (1971), Morfeld et al. (2014; 2016).

Individual animals have unique body proportions and fat distributions (Clements and Sanchez 2015), which may influence BCS and complicate comparisons between individuals. This aspect also seems valid in elephants, and consistent scoring was influenced by variance in an elephant´s individual appearance in many cases. This was especially true for elephants with a very voluminous belly or a prominent thoracic spine, where a vigilant effort was required to remain focused on the lumbar region (Figure 5c). Additionally, the visual scoring approach can hardly discriminate subcutaneous fat and well-developed musculature, which became obvious in elephant males (Figure 5d). Awareness of the musculoskeletal anatomy may reduce this limitation but cannot completely eliminate it. For pet species a muscle condition score (MCS) has been developed to be used complementary to body weight and BCS (Michel et al. 2011; Santarossa et al. 2017). Such systems are based on palpation, which would be impractical in elephants due to their size, thick skin and frequent inaccessibility. Nevertheless, we consider the scoring approach applied here to allow a reasonable ranking of animals.

The scoring of elephant calves represented another challenge. As mentioned before, the applied protocols have not been investigated concerning their applicability in sub-adult elephants. To our knowledge, no comparative research has been conducted in this field yet. Wijeyamohan et al. (2015) report their method to be applicable in elephants independent of sex and age, albeit they do not provide any evidence supporting this recommendation. Although our scoring method turned out to be independent of age, and the overall pattern of a difference between free-ranging and captive animals was also reflected in the calf data (Tables 1 and 2), we remain skeptical whether BCS can be meaningfully applied to growing animals. More insight in the validity of visual BCS in calves and juveniles might be gained by the comparison with growth curves. Hence, a long-term scoring approach combined with weight data would be more informative than our cross-sectional approach.

It remains unanswered how overweight, obesity and the ideal condition in elephants should be defined. For their 10-point scale, Wijeyamohan et al. (2015) do not define which score range is ideal. Morfeld et al. (2014; 2016) define score 3 in their 5-point scale as “ideal/normal”, while Treiber et al. (2012) consider a score from 4 to 7 in their 9-point scale preferable. Consequently for the scale applied here ranging from 0 to 10, a BCS between 4 and 6 could be considered ideal. These definitions are only based on the assumption that the middle range of an index represents a preferable condition. It should be noted that our data on free-ranging elephants indeed suggests that a BCS in the middle of the range, or slightly above it, appears to be the “normal” (Tables 6 and 7).

Scores of European zoo elephants

As intended, data collection and consequent scoring led to a comprehensive overview on BCS of the European zoo elephant population. Our goal to evaluate each zoo elephant in Europe was nearly reached with the evaluation of 97% (518/534). Similar to current results from North America, the majority of European zoo elephants in both species had elevated BCS with 57.7% of the population in the scoring range of 7–10. This percentage is lower compared to the results from North America (73.8%, Table 5).

Relation to findings from previous research

Comparing the average proportions of scoring ranges of individual studies, six studies conducted on African elephants in (semi-) captivity revealed consistently standardised scores of at least 0.6, including three reports with a mean/median of at least 0.8 of the score range. In contrast, research on free-ranging African elephants demonstrated in four out of four cases values of maximally 0.6, with two reports showing higher scores exceptionally during seasons with high primary productivity (De Klerk 2009; Foley et al. 2001). Thus, our findings are in accordance with the literature in reporting higher scores in captive compared to free-ranging African elephants (Table 6).

In nine out of 13 studies investigating Asian elephants in (semi-) captivity, the mean/median BCS was >0.6 of the score range, whereas data on free-ranging Asian elephants reported by Wijeyamohan et al. (2015) and Ranjeewa et al. (2018) had a mean/median of 0.6 respectively 0.51 and our results do not even reach 0.5 (mean: 0.49 and median: 0.45). Our study thus corroborates findings from the literature with higher scores in captive compared to free-ranging populations of the Asian elephant (Table 7).

For wild elephants, body condition scores are affected by seasonal changes in resource availability (Foley et al. 2001; Pokharel et al. 2017; Ranjeewa et al. 2018; De Klerk 2009). Using a sample originating from one of the most extensively studied and best protected elephant populations across Africa, namely in Amboseli National Park, we tried to prevent an overestimation of the difference between captive and free-ranging conditions. Amboseli elephants do fluctuate in body condition but this environment is much less extreme than other habitats, and score changes in a normal (non-drought) year are considered to be minimal (Amboseli Elephant Project, long term data). Similarly, we used a sample from the long-term studied population in Yala National Park for the Asian species.

It is unknown whether the difference in BCS between free-ranging and captive elephants is principally caused by a calorific oversupply or by lack of physical activity. The amount and quality of zoo diets are usually not season-dependent and are more energy-rich compared to natural foods, which might predispose zoo elephants for higher BCS (Hatt and Clauss 2006). Although we cannot explain the negative correlation of BCS with amount of bread fed to female African elephants, the positive correlation of BCS with the amount of fruits and vegetables fed to adult and juvenile Asian elephants supports the above-noted assumption (Table 4). Moreover, the influence of an unnatural energy-rich diet on body condition has been reported in further wildlife species (Heidegger et al. 2016; McWilliams and Wilson 2015; Scheun et al. 2015; Wright et al. 2011). Walking distance in some zoo elephants has been shown to be similar to the situation in the wild (Holdgate et al. 2016; Rowell 2014) although there might be considerable variation between facilities. Results from previous research in the UK and North American zoo population did not reveal any correlation of BCS with daily walking distance (Harris et al. 2008; Holdgate et al. 2016). We were not able to detect a correlation of BCS with staff-directed exercise, as reported by Morfeld et al. (2016). Due to the trend for a shift from direct contact to protected contact in European zoos (EEG 2017), only a few facilities remain that practice staff-directed walking of their elephants. However, a correlation of BCS with management system could also not be detected. This finding corroborates results from North America (Morfeld et al. 2016), but is in contrast to Harris et al. (2008) who reported significantly lower scores for UK zoo elephants managed in free contact. Authors of the latter study do not hypothesise whether this correlation might be caused by staff-directed exercise. In adult Asian elephant females we detected a significant negative correlation of BCS with enclosure size (Table 4). This correlation was not found by Morfeld et al. (2016), but may support the intentions of modern zoos to build larger facilities to further improve elephant welfare. To investigate the influence of such measures in a proper way, a long-term study regarding the development of BCS over time would be more appropriate than our cross-sectional approach applied here. Compilation of comprehensive health data would be important to allow the investigation of potential correlation patterns regarding zoo elephant welfare.

The significantly higher scores found in African elephants compared to their Asian counterparts in European zoos have not been reported yet. Harris et al. (2008) and Morfeld et al. (2016) did not find any difference in BCS between the two elephant species. In contrast to the recent study of the North American zoo population by Morfeld et al. (2016), we could not find any significant correlation between BCS and sex. Neither did differences correlate with reproductive or lactation status. According to findings from previous research in free-ranging populations (Albl 1971; De Klerk 2009; Ramesh et al. 2011), significant differences depending on reproductive and lactation status were expected. Their absence is in accordance with the report from Thitaram et al. (2008) and can be explained by additional nutritional supply of lactating females in captivity, which might cover their increased needs and maintain a stable condition, or the inappropriateness of our cross-sectional study design to detect BCS changes over the course of lactation. On the other hand, we found significantly lower scores in currently breeding adult Asian females compared to non-breeders, and the difference was also significant when all females living in a breeding group (regardless of whether or not the individual animal was breeding) were considered. Such a result would in theory match previous findings in African elephants (Freeman et al. 2009; Morfeld and Brown 2016), black rhinoceros (*Diceros bicornis*) (Edwards et al. 2015) and Asian greater one-horned rhinoceros (*Rhinoceros unicornis*) (Heidegger et al. 2016) that females with a higher body condition score have a lower reproductive viability. However, the finding of Freeman et al. (2009) of a positive correlation of a body mass index (kg/m2) used as indicator of physical condition with the risk to be acyclic in captive African elephant females was not corroborated in either species in the present investigation, which is in accordance to the findings of Chusyd et al. (2018). The interrelationships between breeder status, group size, diet and enclosure size in the present study did not allow identifying a simple causation. Leighty et al. (2009) suggested social complexity and breeding to increase walking rates in zoo elephants, which might explain lower BCS in larger groups that breed and have larger enclosures at their disposal. However, enclosure area might be a surrogate measure for the general investment (in terms of various resources) and other management measures that lead to positive effects for elephant BCS.

Although no indicators of health status have been shown to correlate with BCS in captive elephants yet (Miller et al. 2016), foot disorders and degenerative joint disease in (older) elephants should in theory be exacerbated by high BCS, as suggested by Fowler and Mikota (2006). In other species, reduced longevity and life quality of obese individuals is documented, such as orangutans (*Pongo spp.*) (Cocks 2007), pet dogs (Yam et al. 2016) as well as humans (Samaras and Elrick 2002). Additionally, Heidegger et al. (2016) suggest the occurrence of leiomyomas in captive female greater one-horned rhinos to be linked with obesity; these authors also review some of the pertinent literature for humans. It would be interesting to assess whether this is also true in Asian elephants that often suffer from uterine leiomyoma (Aupperle et al. 2008; Lueders et al. 2010; Sanchez et al. 2004), and which role a potential gene mutation reported in humans may play (Heinonen et al. 2014).

These considerations lead to the recommendation that regular monitoring of weight and body condition, and the implementation of measures that maintain an intermediate rather than an obese body condition, are important in captive elephants. This is not only important with respect to their health in general, but as well to successful breeding. Although the latter may be heavily influenced by factors like availability of appropriate males and herd constellations (Töffels 2015; Wiese and Willis 2006), we consider monitoring of female elephant´s condition an important cue to increase breeding success, which is in accordance with Freeman et al. (2009). This is especially true for the captive population of African elephants which is not self-sustaining (Schwammer and Fruehwirth 2015; Schwammer and Fruehwirth 2016). In long-lived species such as elephants, long-term monitoring is required to reliably detect factors influencing husbandry success with emphasis on their health and welfare.

In conclusion, validated protocols served as practical tools for population-wide visual body condition scoring of European zoo elephants. In accordance with previous research, zoo elephants of both species had significantly higher BCS compared to samples from free-ranging populations. Compared to current population data from North America, zoo elephants in Europe show a trend towards a more ideal scoring range. A near ideal BCS is an aim to strive for as part of welfare in the husbandry of elephants and as such further improvement regarding the diet are warranted for the captive elephant population. To monitor the influence and effectiveness of such adaptations, visual body condition scoring in a long-term approach might present a reliable tool.

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Table S1 Overview of research conducted on body condition scoring in elephants

Albl (1971)	Investigating 240 carcasses of African elephants during cullings in Zambia, this researcher detected a linear negative correlation between the kidney-fat index and the depth of the lumbar depression. Although conducting several morphometric measurements, lumbar depression with the adjoining ridge of the wing of the ilium was the only body region correlating with an elephant´s physical condition. During dry season elephants showed a poorer condition compared to the wet season. No universal body condition score index was defined.
Poole (1989)	Used a simple visual method focused on the shoulder blade, the pelvic bone and the backbone to determine changes during musth. No universal body condition score index was defined.
Godagama et al. (1998)	Applied a previous version of the index subsequently published by Wemmer et al. (2006) in 140 (68 females, 72 males) captive elephants in Sri Lanka. These elephants were private owned or temple elephants and covered all age categories (3-75 years). The authors reported a significant difference in BCS between females and males with higher scores in females. No significant correlations of BCS with age or husbandry circumstances were detected.
Foley et al. (2001)	Evaluating effects of stress in free-ranging African elephants, body condition was categorized from 1 (emaciated) to 5 (no bony structures visible). According to the findings from Albl (1971) scoring was based mainly on the lumbar region. A correlation pattern between body condition and season was demonstrated with lower values during the dry season. Lowest scores occurred in late dry season. Foley et al. (2001) explain this pattern with seasonal variation of diet quality and availability.
Wemmer et al. (2006)	Worked out a method to assess body condition in Asian elephants, deriving a numerical index by separate visual assessment of six different body regions (head, scapula, thoracic region, flank area, lumbar vertebrae, pelvic bone). Thus a total score between 0 and 11 can be obtained and interpreted. She tried to correlate the measured body condition scores with morphometrically determined variables for the amount of subcutaneous fat, but could not find any location that closely parallels the numerical index. Application of the scoring system on a sample of 119 juvenile and young adult Asian elephants in Forest camps in countries of origin. No significant correlations between body condition score and age or sex of the elephants were detectable.
Harris et al. (2008)	Investigated, during the report on the welfare of zoo elephants in the United Kingdom, beside numerous other variables, the body condition. They did so without former protocol and based their interpretation on comparisons with photographs from the wild and experience of the examiner. Thereby they focused on the rear view of the elephant and chose the spinal protrusion, hip visibility, roundness of the body and the thighs as expressive features. Scores from 1-5 were assigned to pictures, considering a value of 3 to be normal. Doing so, only 6 of the 70 scored individuals were found in desirable condition. Subsequently the group tried to correlate body condition scores with species, sex, age, origin, management system and measured cortisol metabolites. Only management system showed a significant correlation with lowest scores in free contact and highest ones in no contact systems. The authors do not formulate any explanation for this correlation. Any other variable seemed to be independent from body condition.

Thitaram et al. (2008)	Evaluated the body condition of 22 female Asian elephants in two Elephant camps in Thailand during their study on estrous cycle lengths. They used the protocol formulated by Wemmer et al. (2006) and found scores ranging from 6.5 to 10. Thitaram et al. (2008) found no markedly different body condition of normal and irregularly cycling elephants. They report the absence of an estrous cycle in the elephant cow with the lowest BCS (6.5) of the studied population.
Velthuizen (2008)	Applied Wemmers method in the investigation of body condition changes in seven African elephants kept in a training facility in South Africa. The investigation led to no reliable results, which is due to a suboptimal study design according to the researcher.
De Klerk (2009)	Used Poole's (1989) method during her study on free-ranging populations in the Eastern Cape Region, South Africa to show correlations with resource qualities. In doing so, lower body condition scores in populations with limited dieatry resources, during seasons with lower primary productivity, and in lactating females were demonstrated.
Fernando et al. (2009)	Used a simplified version of Wemmer et al.'s (2006) index in order to assess the body condition of free-ranging Asian elephants involved in the human-elephant-conflict. The researchers took 5 reference photographs of free-ranging individuals representing almost the entire spectrum of body conditions. They assigned the scores 1, 3, 5, 7, 9 to the pictures. In that way the scale can be extended by 0 and 10 if necessary and conditions localized between the given photographs will be evaluated with 2, 4, 6 or 8. Considering its simplicity and the inevitable subjectivity in assessing, they found a comparatively small error in the application of the method.
Pinter-Wollman et al. (2009)	In order to monitor physiology of translocated elephants in Tsavo East National Park, Kenia, a modified protocol of Wemmer´s index was applied. Scores of 544 adult individuals revealed significantly higher values for local compared to translocated elephants. Females showed a significantly lower condition than males. During wet season BCS´s were significantly higher than during dry season.
Ramesh et al. (2011)	Used Wemmer et al.'s (2006) body condition score index as basis, modifying and combining it with the technique described for ungulates in general by Riney (1960). In doing so, they added a seventh body region to Wemmer et al.'s (2006) index and determined a total score range from 1-14. With this protocol they assessed the body condition of 1622 free-ranging elephants in Mudumalai Tiger Reserve, Western Ghats, India. The results show a significant correlation between the assigned values and the season, with higher scores during the wet and decreased ones in the dry season. As cause for this phenomenon the changes in availability of food resources for the elephants ar mentioned. The authors conclude that body condition scores may be useful as sensitive health indicators in elephants and encourage such studies over larger populations to develop reference values.
Treiber et al. (2012)	Took the correlation between body condition and several diseases for granted and used a 9-point scale for her evaluations on Asian elephants. Their index corresponds well with the previously published indices, although trying to enhance details. Moreover they correlate body condition scores to and validate them with ultrasonic rump fat measures.

Morfeld et al. (2014)	Published the development of a new visual body condition scoring index for the assessment of body fat and condition in female African elephants. Compared to Wemmer et al.'s (2006) method, they reduced the observed body regions from 6 to 3, which they chose by their correlation with the local ultrasonic subcutaneous fat thickness. These areas are the backbone, the pelvic bone and the ribs. The developed method was subsequently applied in a comparison of body condition scores assigned to photographs from samples of female zoo elephants and their free-ranging counterparts. The comparison revealed significant lower values in the free-ranging elephants. Following previous studies, the authors expected a relationship between high body condition scores and the poor reproductive activity in zoo elephants (Clubb et al., 2009; Dow et al., 2011; Freeman et al., 2009; Taylor and Poole, 1998). They recommend the use of body condition scores in the medical management and optimization of husbandry practices in zoo elephants, potentially leading to a more healthy and sustainable population.
Kumar et al. (2014)	Ascribed a BCS to the 12 (4 males, 8 females) zoo-kept Asian elephants investigated during their endocrinological study in southern India. Using the index from Wemmer et al. (2006), they report values ranging from 4 to 9. They could not find any significant correlation between the body condition and any of the measured faecal hormones. Moreover they could not find any significant variation of the body condition with the age or facility of the individual elephants.
Romain et al. (2014)	Used the index described by Fernando et al. (2009) to measure the body condition of captive Asian elephants in Thailand, but laying their study emphasis on the diet composition and food intake, the body condition score values were of minor interest.
Wijeyamohan et al. (2015)	Took the indices from Wemmer et al. (2006) and Fernando et al. (2009) as basis for the development of a visual system for Body Condition Scoring of Asian elephants. They demonstrated the applicability of this system in free-ranging as well as in captive elephants and provided an exemplary photograph for every score. Moreover they proved the significant correlation between BCS values and morphometric estimates of body fatness. According to this publication, the developed system facilitates the reliable assessment of Asian elephants independent of age and sex. Investigating captive elephants in the USA and a Sri Lankan population, they found on average a two point higher BCS in the American population.
Morfeld et al. (2016)	Being part of the project “Using science to understand zoo elephant welfare”, body condition of 240 elephants in North American zoos was assessed. Before applying the established 5-point score for the African elephant in the Asian species, biological validation was performed by measuring serum triglyceride levels. Results found 34% of the assessed zoo elephants in the highest score (=5) and 40% with a BCS of 4. This means that 74% of zoo elephants showed a physical condition considered as overweight or obese. Increased diversity in feeding methods and being female occurred as risk factors for an elevated score. In contrast, an unpredictable feeding schedule and staff-directed walking for more than 14 hours per week were associated with a decreased risk for elevated scores.
Schiffmann et al. (2017)	This study reviewed existing visual body condition score protocols for elephants. Additionally a test based on pictorial documents compared different scoring approaches. Results led to the conclusion that body condition scoring in elephants may be best completed using overview and/or algorithm methods.

Pokharel et al. (2017)	Investigation of 653 free-ranging Asian elephants in India revealed a correlation of BCS and season with higher scores during the wet season. In females BCS was negatively correlated with feacal glucocorticoid metabolites. BCS development of nine adult females was observed over the course of seven years with the detection of distinct annual changes.
Chusyd et al. (2018)	This research group investigated the relationship between adiposity and reproductive cycling in 20 female African elephants living in North American zoos. They checked for patterns of BCS as well and found positive correlations with age, body mass and fat mass. No significant influence on cycling could be found.
Ranjeewa et al. (2018)	Body condition of adult female (N=218) and sub-adult and adult male (N=329) elephants in the Udawalawe National Park were assessed by a protocol modified from Wemmer et al. (2006). A mean score in the middle of the range was determined (7.68 ± 3.04). Scores of females and males showed a significant difference with higher values in males. Considering various age-size classes of the latter, mature-adult males had the lowest scores and young-adult males the highest with sub-adult males ranking between them. The authors demonstrate a significant inverse correlation of elephant body condition with reservoir water level. They explain this phenomenon by the lush grass growing on the banks of the reservoir in times of low water levels.

Table S2 Overview of research conducted on body condition scoring in elephants and reported correlation with further parameters (Table modified and extended from Schiffmann et al. (2017))

Living conditions	Applied Index (scoring range)	N	Average score	Standardized average score (average score/scoring range)	Correlating parameters	Kind of correlation	Remarks	Reference
African elephant (*Loxodonta africana*)								
Free-ranging								
free-ranging	kidney-fat index, depth of lumbar depression, (good, fair, poor)	240	-	-	season	lower condition during dry season	especially well developed fat reserves in pregnant cows	Albl (1971)
free-ranging	new developed (1-6)	22	-	-	stage of musth	body condition decreases during musth phase	exclusively males in musth considered	Poole (1989)
free-ranging	concavity around lumbar depression and scapula (1-5)	not indicated	mean: 2.8-4.01	0.56-0.80 (mean)	season	lower body condition during dry season	sample size and composition not indicated	Foley et al. (2001)
free-ranging	extended the index from Poole (1989) (1-8)	4-107 (depending on season and category)	mean: 3.2-5.6 (depending on season and category)	0.40-0.70 (mean)	season	lower scores during seasons with decreased primary productivity	-	De Klerk (2009)
					limitation of nutritional resources	lower scores in population with limited resources	-	
					lactation	lower scores in lactating females	-	
free-ranging	modified from Wemmer et al. (2006) (0-2)	544	-	-	season	lower scores during the dry season	only adults considered	Pinter-Wollman et al. (2009)
					sex	lower scores in females	only adults considered	
					history of translocation	lower scores in translocated elephants	only adults considered	
free-ranging	new developed (1-5)	57	3 (1-5)	0.60 (median)	captive vs. free-ranging	significantly higher in captive elephants	investigation on female elephants only	Morfeld et al. (2014)

Semicaptive and captive								
semicaptive[a]	Wemmer et al. (2006) (0-11) and a digital index (not published)	7	mean and median: 10	0.83 (mean and median)	-	-	suboptimal study design lead to no reliable results	Velthuizen (2008)
captive[b]	own index (5-1)	not indicated	mean: 2.0	0.60 (mean)	handling method	significantly thinner when managed in free contact compared to no contact	-	Harris et al. (2008)
captive[c]	new developed (1-5)	50	median: 4 (2-5)	0.80 (median)	captive vs. free-ranging	significantly higher in captive elephants	investigation on female elephants only	Morfeld et al. (2014)
captive[c]	Morfeld et al. (2014) (1-5)	132	median: 4; mean: 4.00	0.80 (mean and median)	sex	higher scores in females	-	Morfeld et al. (2016)
					staff-directed walking exercise	decreased risk for higher scores	only significant if exercise exceeds 14 hours per week	
					unpredictable feeding schedule	decreased risk for higher scores	-	Morfeld et al. (2016)Morfeld et al. (2016)
					diversity in feeding methods	increased risk for higher scores	-	
captive[c]	Morfeld et al. (2014) (1-5)	20	median: 4; mean: 3.85	0.77 (mean), 0.80 (median)	age	positive	females only	Chusyd et al. (2018)
					body mass	positive		
					fat mass	positive		

Asian elephant (*Elephas maximus*)								
Living conditions	**Applied Index (scoring range)**	**N**	**Average score**	**Standardized average score (average score/scoring range)**	**Correlating parameters**	**Kind of correlation**	**Remarks**	**Reference**
Free-ranging								
free-ranging	new developed (0-10)	-	-	-	-	-	-	Fernando et al. (2009)
free-ranging	combined indices from Wemmer et al. (2006) and Riney (1960) (14-1)	1622	-	-	season	decrease in body condition during dry season	significant differences between age-classes	Ramesh et al. (2011)
					sex	higher body condition in males	demonstrated for adult elephants only	
free-ranging	new developed (1-10)	27	6 (median and mean)	0.60 (median and mean)	captive vs. free-ranging	higher in captive elephants	application of index recommended independently of age and sex	Wijeyamohan et al. (2015)
free-ranging	Morfeld et al. (2014) (1-5)	653	-	-	season	lower scores more frequent during dry season	-	Pokharel et al. (2017)
					faecal glucocorticoid metabolites (fGCM)	fGCM levels highest in individuals with lowest BCS		
free-ranging	modified from Wemmer et al. (2006) (0-14)	3175 (containing 526 individual elephants at different points of time)	mean: 7.68	0.51 (mean)	reservoir water level	higher condition during season with lower water level	only adult and sub-adult elephants considered	Ranjeewa et al. (2018)
					sex	higher scores in males	only adult and sub-adult elephants considered	

Semicaptive and captive								
semicaptive[d]	previous version of the index by Wemmer et al. (2006) (0-11)	140	Median: 7; mean: 6.95	0.58 (mean and median)	sex	higher body condition in females	-	Godagama et al. (1998)
semicaptive[e]	new developed (0-11)	119	mean: 7.3	0.61 (mean)	-	-	no correlation with further parameters detected	Wemmer et al. (2006)
captive[b] and semicaptive[f]	own index (5-1)	semicaptive: 42; captive: not indicated	semicaptive mean: 3.25; captive mean: 2.1	semicaptive: 0.35 (mean); captive: 0.58 (mean)	captive: handling method	captive: significantly thinner when managed in free contact compared to no contact	-	Harris et al. (2008)
semicaptive[g]	Wemmer et al. (2006) (0-11)	22	median: 8.75; mean: 8.70	0.73 (mean and median)	-	-	mature females only; the female with lowest score (6.5) was the only one not cycling	Thitaram et al. (2008)
captive[c]	new developed (1-9)	12	median: 6.25	0.69 (median)	rump fat thickness	positive linear	fat thickness measured by ultrasound	Treiber et al. (2012)
captive[h]	Wemmer et al. (2006) (0-11)	12	median: 8; mean: 7.25	0.60 (mean); 0.67 (median)	-	-	-	Kumar et al. (2014)
captive[i]	Fernando et al. (2009) (0-10)	10	median: 6; mean: 6.3	0.57 (mean); 0.55 (median)	-	-	-	Romain et al. (2014)
captive[c]	new developed (1-10)	31	8 (median and mean)	0.80 (mean and median)	captive vs. free-ranging	higher in captive elephants	application of index recommended independently of age and sex	Wijeyamohan et al. (2015)
captive[c]	new developed (1-5)	108	median: 4; mean: 4.05	0.81 (mean); 0.80 (median)	sex	higher scores in females	-	Morfeld et al. (2016)
					staff-directed walking exercise	decreased risk for higher scores	only significant if exercise exceeds 14 hours per week	
					unpredictable feeding schedule	decreased risk for higher scores	-	
					diversity in feeding methods	increased risk for higher scores	-	
semicaptive[g]	Wemmer et al. (2006) (0-11)	5	median: 8; mean: 7.6	0.63 (mean); 0.75 (median)	-	-	exclusively males considered , no effect of GnRH-vaccination on BCS detected	Somgird et al. (2016a)

semicaptive[j]	Wemmer et al. (2006) (0-11)	9	median: 8; mean: 8.33	0.69 (mean); 0.75 (median)	duration of musth phase	Positive	exclusively males considered	Somgird et al. (2016b)
					age	positive but not significant	exclusively males considered	

c: investigated animals live in captivity, sc: investigated animals live in semi-captive conditions in countries of origin, f: free-ranging individuals were investigated a: Elephant training facility in South Africa; b: UK zoos; c: North American zoos; d: Private owned and temple elephants in Sri Lanka, e: Forest camps in India, Nepal and Myanmar; f: Indian working camp and Wildlife rehabilitation centre; g: Elephant camps in Thailand; h: South Indian zoos; i: Zoos in Thailand; j: Elephant conservation center in Thailand

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Zusatzteil mit Angaben zu weiteren Forschungsarbeiten

Body Condition Scores (BCS) in European zoo elephants' (*Loxodonta africana* and *Elephas maximus)* lifetimes – a longitudinal analysis

Christian Schiffmann, Marcus Clauss, Stefan Hoby, Daryl Codron, Jean-Michel Hatt

In press in the *Journal of Zoo and Aquarium Research*

Die Body Condition Scores der Zooelefanten Europas wurden auch hinsichtlich ihrer Entwicklung im Laufe des Lebens eines Individuums analysiert.

Original Research Article

Body Condition Scores (BCS) in European zoo elephants' (*Loxodonta africana* and *Elephas maximus)* lifetimes – a longitudinal analysis

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Abstract

In further improving zoo elephant welfare, the diet and feeding regime are key factors. Together with the encouragement of physical activity, they may support the management and prevention of overweight and obesity, which are considered a common concern in zoo elephants. Besides weight monitoring, visual body condition scoring (BCS) has proven a practical tool for the assessment of (zoo) elephants' physical condition. From the individual management as well as the medical perspective, documentation of an elephant´s BCS change over time might be much more informative than a population-wide cross-sectional analysis. We present a compilation of cases where European zoo elephants´ BCS can be compared to influencing factors such as reproductive activity, physical disorders, advanced age, stressful situations and diet adaptations. Our study of the European zoo elephant population describes the reflection of various life circumstances and management adaptations in the BCS of individual elephants, and changes of population-wide BCS over time. An online archive to build up a reliable, individual-based data basis with minimal additional workload for elephant-keeping facilities is introduced.

Introduction

With respect to their physical size, mental capabilities, conservation status and public perception as charismatic individuals, management of captive African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) is a challenging task. Compared to dietary resources in the wild, feeding regimes in zoo elephants are presumed to often oversupply energy, leading to obesity. Although there are no established guidelines as to when to call an elephant "obese" or "overweight", the terms have often been used in relation to elephants with high BCS or body mass (Clubb and Mason, 2002; Harris et al., 2008; Hatt and Clauss, 2006; Morfeld et al., 2014; Morfeld et al., 2016). Therefore, body condition monitoring is an important part in elephant management and preventative care. This can be done by regular weighing on a scale or by visual body condition scoring (BCS). The latter is considered a useful method to reliably assess (zoo) elephants (reviewed in Schiffmann et al., 2017).

Several indices have recently been developed for elephants and applied in free-ranging as well as semi-captive and captive populations (Fernando et al., 2009; Morfeld et al., 2014; Morfeld et al., 2016; Treiber et al., 2012; Wemmer et al., 2006; Wijeyamohan et al., 2015). Scores have been reported to be affected by age (Chusyd et al., 2018; Somgird et al., 2016), sex (Godagama et al., 1998; Morfeld et al., 2016; Pinter-Wollman et al., 2009; Ramesh et al., 2011), living conditions (Morfeld et al., 2014; Schiffmann et al., 2018; Wijeyamohan et al., 2015), season (Albl, 1971; De Klerk, 2009; Foley et al., 2001; Pinter-Wollman et al., 2009; Pokharel et al., 2017; Ramesh et al., 2011; Ranjeewa et al., 2018), husbandry parameters (Harris et al., 2008; Morfeld et al., 2016), reproductive status such as lactation (De Klerk, 2009), history of translocation (Pinter-Wollman et al., 2009), stress level (Pokharel et al., 2017) and duration of musth (Poole, 1989; Somgird et al., 2016).

As of today, only a single study investigated the BCS change over time in (free-ranging) elephants (Pokharel et al., 2017), indicating a seasonal fluctuation of BCS with available resources. Considering the methodological advantages (reviewed in Schiffmann et al., 2017), visual BCS might represent a practical monitoring tool. Nevertheless, its usefulness in the longitudinal perspective needs further validation. It is the aim of this study to evaluate the applicability of BCS in a longitudinal approach in zoo elephants. We do this on the individual elephant basis similar to the current work on free-ranging female Asian elephants (Pokharel et al., 2017), but emphasize the influence of specific potentially demanding periods (e.g. pregnancy, lactation, physical disorders, disturbances, transfers) in a zoo elephant's life. Given that a continuous historical photographic documentation of zoo elephants' body condition is rare, our evaluation opportunistically focuses on cases where such documentation coincided with specific events or circumstances. Additionally, we investigate the change over time of BCS in a population-wide perspective for European zoo elephants. We demonstrate the method's sensitivity and propose recommendations for the application of BCS as monitoring tool in elephant management and care.

Material and Methods

Our method of data collection and criteria regarding standardization of a pictorial document are extensively documented in a previous publication (Schiffmann et al., 2018). Besides our own photograph and life history data collection, we searched every accessible archive or database in elephant-keeping zoos regarding helpful pictorial documents. As indicated in a previous report (Schiffmann et al., 2018), there were only a few facilities conducting regular photographic body condition documentation at the time of the study; therefore, archived photographs were not consistently available. Additionally, private archives were used where access was allowed. Data collection took place between beginning of January 2016 and end of March 2017. To be included in the study, a pictorial document had to fulfill the following criteria: (i) datable to a month (where an accurate date was missing, the 1st day of the month was recorded); (ii) clearly identifiable individual; (iii) sufficient recognition of the relevant body regions (backbone, pelvic bone, ribs) from a lateral perspective. Moreover (iv), the elephant had to be pictured in a standing or moderate walking body position to allow a reliable assessment. We additionally (v) defined resolution of the photograph to be sufficient if recognition of the generic wrinkles on the skin surface of the elephant was possible. If this was ensured, we assume, the pictorial documents quality allowed the evaluation of the critical bony structures. Finally (vi), distinct patterns of shade or masses of hay, straw and other substrates on the back of the elephant may make any assessment impossible. Likewise, bright sun light straight from the side can reduce the picture contrast to such a degree, that the mandatory fold right beside the tail head cannot be judged. Such documents were excluded from the study. Life histories of individual elephants (date of birth, required to calculate the age at the time a specific picture was taken, as well as dates of calving or transfers), were taken from the current studbooks (Schwammer and Fruehwirth, 2016; van Wees and Damen, 2016).

Body condition scoring

To assign a consistent BCS to every photograph, we used a protocol in which the species-specific indices for African elephants from Morfeld et al. (2014) and for Asian elephants from Fernando et al. (2009), Wijeyamohan et al. (2015) and Morfeld et al. (2016) were assembled in an overview approach as detailed in Schiffmann et al. (2017). According to recently published findings in dairy goats, scoring results may reach a higher reproducibility and repeatability by the use of example drawings as opposed to example pictures (Vieira et al., 2015). Therefore, we had drawings made for every score and each species, showing the elephant in side profile as well as at an angle from behind. These drawings served as the principal basis for the scoring. The score of the drawing looking most similar to the photograph under examination was assigned to each individual elephant. The focus was laid on the visibility of indicated bone structures of the lumbar region, which have been shown to correlate best with the amount of body fat in elephants (Albl, 1971; Morfeld et al., 2014; Morfeld et al., 2016). In addition, the overall appearance of the elephant was taken into account and was considered more important than single characteristics (e.g. visibility of ribs or edges of the scapula). This approach is in accordance with the findings of a recent review on various scoring indices developed for elephants (Schiffmann et al., 2017). All elephants were scored by the first author. To reduce potential bias by scoring serial pictures from the same location, photographs were scored in a random order. The latter was achieved by automatically sorting them according to an independent variable (technical size of the picture). Although the scoring was performed blinded, recognition of an individual elephant or the location by the examiner could not be excluded. Scoring of the photographs was done prior to further data analysis, and the method for intra-examiner agreement had been checked as previously reported (Schiffmann et al., 2018).

Data for individual elephants

To facilitate comparison of scores between individuals, each score was linked to age measured in months of life of the assessed elephant. Where more than one score per month of life was available, we calculated the mean. Subsequently we plotted the scores against the months of life for each elephant. By checking the resulting multitude of graphs for reoccurring patterns, we selected only individual elephants with comprehensive data (BCS photographs and life history information) available for further display and interpretation. Therefore, even though a much larger number of European zoo elephants has undergone conditions such as pregnancy, birth, lactation, transfer to another facility or another enclosure, or disease, we were limited to those cases where these conditions or events fell into a period for which, for the elephant in question, sufficient (historical) photographic documentation was available. Potentially correlating factors were not determined a priori, but recorded during data collection and investigated when the the availability of data provided the opportunity to do so. According to literature data, duration of lactation was assumed to be 36 months, although individual differences may exist (Abbondanza et al., 2013; Moss et al., 2011). Sufficient data for a statistical evaluation of a specific life history event on BCS was only available for females giving births; in 10 cases, BCS scores from the time of 3 months prior to birth, and from the time of 3 months after birth, were available. These scores were compared by Wilcoxon test for paired samples. Note that because individual BCS scores represent data that is not continuous, nonparametric statistics need to be applied by default. To preserve anonymity in displaying individuals, identifiers such as studbook numbers or names are not included in this publication.

Population-wide perspective

To check if there is a seasonal variation in BCS in the European zoo elephant population, a sample of pictures taken during spring time (between beginning and ending of March; reflecting potential changes in

BCS reflective of winter) was compared to a sample originating from the beginning of winter time (between beginning and ending of October; reflecting potential changes in BCS reflective of summer). We considered all age classes in this comparison, but with respect to a potential bias by growing elephants, we restricted this analysis to adults (> 15 years), comparing spring and autumn data using the Mann-Whitney-U test. Because we did not control for the presence of individuals in March and October data but used all available data, regardless of whether an individual occurred in both seasons or only one season, this approach must be considered exploratory. In a second, more restricted approach, we only used data on individual elephants taken from spring and autumn of the same year, accepting only one pair of values per animal, but different years across animals; these data were assessed by the Wilcoxon test for paired samples.

Additionally, we investigated the change over time of population-wide BCS, calculating the annual average of each elephant´s score. This allowed the calculation of annual mean scores for the African and Asian species. We considered the time span between 2000 and 2017 in this analysis, regressing BCS over year to test for a significant effect of time on the mean BCS. Because elephant age could influence the BCS, we included this variable as a covariate in the analysis, using General Linear Models (GLM). Because of the potential for autocorrelation within this time series, we compared model results with autoregressive (AR) models including first an AR co-efficient of 1 (i.e. BCS at *t*-1, where *t* is the year), and then both AR(1) and AR(2) as additive effects. The trend is considered to deviate from the null hypothesis if H_0 is rejected ($\alpha = 0.05$) in AR(0), AR(1) and AR(2). Higher-order AR coefficients were not tested because of the relatively short time series and the fact that with each additional co-efficient the series becomes even shorter. GLMs were analyzed using the lm function of R 3.4.2 (Team, 2017). These analyses were performed, in sequence, across all individuals, for each species separately, and then for each species and sex separately, to interrogate the generality of results obtained.

Results

Collection of pictorial documents

In total, 64 different facilities maintaining 140 African and 228 Asian elephants were visited (all by the first author) on site between beginning of January 2016 and the end of March 2017. Together with photographs received by mail, 192 African and 326 Asian elephants of European zoos were included in this study. This sample consisted mainly of elephants participating in the European Endangered Species Programs (EEP´s) (470/518=91%), but elephants of non-member facilities (48/518=9%) were included as well. Altogether, a total of 8 200 pictorial documents of European zoo elephants were selected according to the aforementioned criteria. They were sampled between September 1982 and the end of March 2017. The number of pictures showing an individual elephant ranged from one to 79. The covered extent of an elephant´s period of life varied heavily between individuals (range: 1-482 months, mean: 121 ± 75.67 months).

Life history data collection

Documentation and availability of life history and husbandry data varied considerably between institutions. As expected, comprehensive husbandry data were received only during on-site visits. Seven institutions had established BCS protocols, but only four of these zoos documented body scores with photos. Where dietary and management adaptations were documented, corresponding data were extracted from the keeper´s diary. Data on physical disorders were gained from published work, from veterinarians in charge or their medical records, where access was allowed. Data on occurrences of births and inter-zoo transfers were taken from the current studbooks (Schwammer and Fruehwirth, 2016; van Wees and Damen, 2016).

(I) Data display for individual elephants

Distinct BCS patterns over time were detectable in (A) calves (< 5 years), (B) females during pregnancy and lactation, (C) diseased elephants, (D) aged elephants (> 40 years) and (E) after significant adaptations in management and/or diet.

A) Calves (< 5years)

In calves BCS appeared stable and high (around 7-8/10) during their first 60 months of life. This pattern occurred in females and males of both species and could be documented for 14 of 15 calves for which more than 10 BCS scores were available. Representative graphs are displayed in Fig. 1 and further cases are provided in the supplementary material (Fig. S1).

B) Females during pregnancy and lactation

No consistent BCS change during pregnancy and lactation was detectable (Fig. 2 and 3). Lowest scores regularly occurred between month 1 and 100 after giving birth, but not consistently in all breeding females, and also not consistently within individual females. The females displayed in Fig. 2 and 3 represent 10 of 25 individuals for which such data was available. The selected graphs are representative for all 25 cases as can be inspected in the supplementary material (Fig. S2). In the ten females for which BCS were available both three months prior to, and three months after birth, there was no significant difference between there time points (medians of 7.0 and 6.6, respectively, P=0.091).

C) Diseases

Several diseased elephants showed a marked decrease in BCS during the (first) occurrence of clinical signs (Fig. 4). When the underlying disorder was treated and a healthy condition reestablished, BCS reached levels similar or even higher than the individual baseline before the disease (Fig. 4 b + c).

D) Advanced age (> 40 years)

In elephants exceeding their 480th month of life, a continuous decrease in BCS was commonly detectable (in 24 out of 38 elephants in this age range, while 12 of the remaining 14 individuals showed a steady and two an increasing condition). This decrease varied in its pattern (time of beginning, incline) between individual elephants (Fig. 5). Graphs from the cases not depicted here can be inspected in the supplementary material (Fig. S3).

E) Stressful periods, transfers and diet adaptations

A stressful period due to the construction of a new exhibit with the elephants remaining on site (Hoby et al., 2015) led to a temporary depression in BCS in three out of four female African elephants in one facility (Fig. 6). The influence of transfer on BCS was obvious in two Asian males. While an adult male continuously gained condition at his new location (Fig. 7a), a young male expressed a temporary depression after his introduction into a bachelor group (Fig. 7b). Diet changes with an increase in roughage and a decrease in concentrates and introduction of feeding enrichment was reported by two facilities (keeping 0.3 adult *L. africana* respectively 2.6 adult *E. maximus*). In both cases, the influence of the new feeding regimens was detectable by progressively decreasing BCS (Fig. 8 and 9).

(II) Data analysis European zoo elephant population regarding season and change over years

No significant season-dependent variation in BCS between spring and autumn was detectable, neither in the African nor the Asian species of the European zoo elephant population, regardless of whether all available data (*L. africana*: P=0.224; *E. maximus*: P=0.508) or only data from the same individuals within the same year (*L. africana*: P=0.136; *E. maximus*: P=0.930) were assessed.

During the considered years (2000-2017) the total number of available scores per year ranged from 16 to 272. Population-wide annual mean scores showed a trend towards lower values over time (Fig. 10). While this effect was significant (p<0.05) when yearly averages for all individuals were taken together, further interrogation of the dataset revealed that significance was only evident in *E. maximums* (Table 1). Moreover, within *E. maximus*, only females actually showed a significant trend of decreasing BCS over time. These results were consistent across models with and without autoregression co-efficients (which themselves almost never produced slopes different from zero), hence we can be confident that any temporal autocorrelation in these series is negligible. Animal age also had no significant influence on BCS once the year of data collection was accounted for.

Discussion

To minimize the effect of inherent subjectivity of visual body condition scoring, the evaluation of the pictures was restricted to one single examiner, and a formalized scoring protocol was applied. Moreover, the results from our previous study support the repeatability of the applied scoring method (Schiffmann et al., 2018). Our compilation allowed the association of influencing factors and management adaptations with an individual elephant´s BCS as well as the population-wide change over the course of years.

The amount of available pictorial and life history data varied significantly between facilities. Reliable results are expected exclusively in cases for which additional data were available. Thus, our descriptions and interpretations are biased towards elephants/institutions with more extensive documentation. We cannot exclude that this circumstance led to the over- or underestimation of certain aspects. Therefore, our conclusions might not be considered invariably representative for the entire zoo population.

(I) Data display for individual elephants

(A) Calves

Between birth and month 60 of life, a zoo elephant´s BCS remained stable on a score 7-8/10 (Fig. 1). Elephant calves are significantly growing in height and weight during this period of life (Kurt and Kumarasinghe, 1998; Kurt and Nettasinghe, 1968; Lee and Moss, 1995; Shrader et al., 2006; Weihs et al., 2001). It can be speculated whether the method of visual scoring is not sufficiently sensitive to detect variations in this stage of life. On the other hand, dietary supply and health conditions are expected to be ideal in young zoo elephants and a constant BCS may be the consequential result. In addition, reduced variance in BCS of calves and sub-adults compared to adults have been reported in free-ranging Asian elephants as well (Ramesh et al., 2011; Ranjeewa et al., 2018). By implication, a significant deviation of this BCS pattern in zoo elephant calves might indicate diet or health inadequacies. Elephant calves up to 5 years of life should probably not vary significantly in BCS under zoo conditions. This hypothesis is linked to the assumption that the very high BCS observed in calves should then become lower during puberty.

Although very limited in sample size, some graphs for young sub-adults (5-10 years) appear to corroborate this concept (Fig. 11). Collection of more comprehensive data of calves born in European zoos during the past years might provide the basis to confirm or reject this hypothesis in the near future.

(B) Females during pregnancy and lactation

According to our knowledge, the influence of pregnancy and lactation on BCS in zoo elephants has not been investigated. Higher energy requirements during lactation lead to the expectation of lower scores in the 36 months after giving birth. This correlation has been confirmed in free-ranging African elephants (Albl, 1971; De Klerk, 2009). In our cross-sectional population-wide investigation we found differences in BCS between females of breeder and nonbreeder status in Asian elephants, but we did not detect differences between pregnant or lactating individuals (Schiffmann et al., 2018). In accordance with this finding, no distinct BCS pattern on the individual elephant basis occurred here. Although several females expressed higher scores pre- compared to post-partum, this pattern was not consistent, and some elephants remained on a constant level independent of pregnancy/lactation (Fig. 2 and 3). Again, it is questionable whether visual scoring is not sufficiently sensitive, or whether the elephants remain in a stable condition despite the varying energetic demands. The latter might be explained by the compensation of additional costs through an energy-rich diet provided under zoo conditions (Hatt and Clauss, 2006). In two Asian females with exceptionally short inter-calving intervals (3 years or even shorter), a continuous decline in BCS over the years was evident (Fig. 3c + d). It can be questioned whether such short inter-calving intervals are ideal for the female´s health, and whether it would be preferable to let them breed every 4-5 years only. While limited dietary resources and/or population density are supposed to extend inter-calving intervals in the wild (Moss et al., 2011; Slotow et al., 2005; Wittemyer et al., 2007), such constraints are lacking in captivity. Regeneration periods for female elephants might be recommendable in captive breeding management.

(C) Diseased elephants

The impact of injuries on body condition in two free-ranging male African elephants have been reported in the literature (Ganswindt et al., 2010). We demonstrate a similar pattern in four zoo elephants (one African and three Asian) affected from digestive tract disease (Fig. 4). Interestingly, in two cases with ultimate resolution of the underlying disorder (molar malocclusion, acute bacterial infection), BCS subsequently reached even higher levels than prior to the incident (Fig. 4 b + c). On the other hand, this rebound did not occur in chronic persisting disorders (recurrent colic, hepatopathy and suspected chronic renal failure) (Fig. 4 a + d). Change over time of BCS in these cases indicates the capability of visual scoring as a tool for medical monitoring in elephants. To determine the sensitivity of this approach in comparison or in combination with weight monitoring or regular blood work, further research is needed. In doing so, the potential impact of age should be considered and interpretations adjusted correspondingly.

(D) Aged elephants

In elephants over 40 years of age we repeatedly detected a continuous decrease in BCS (Fig. 5). This loss in condition might be caused by age-related alterations (e.g. molar abrasion) or disease. In the cases demonstrated here, no diseases were diagnosed. Literature on the correlation between BCS and age in elephants is very scarce. In 9 semi-captive male Asian elephants of advanced age (45-67 years; average 58.5 ± 8.5years) Somgird et al. (2016) demonstrated a positive (non-significant) correlation between BCS and age, which corroborates with the findings by Chusyd et al. (2018) in a sample of 20 adult female African elephants (16-51 years; average 34.75 ± 8.17 years) living in North American zoos. In a cross-sectional population-wide analysis of European zoo elephants we could not find any correlation between age and BCS (Schiffmann et al., 2018). We hypothesize a life-stage dependent variation of this correlation in elephants and consider further research on this subject recommendable. Especially in geriatric and potentially multi-morbid elephants, regular BCS documentation might be a valuable tool for repeated evaluation of their health state and quality of life. The latter is of increasing importance in zoo animal medicine when dealing with the management of geriatric individuals (Hatt, 2017).

(E) Stressful periods, transfer and diet adaptations

A correlation between reduced physical condition and elevated stress indicators has been suggested for wildlife species including Asian elephants (Lane et al., 2014; Pokharel et al., 2017; Scheun et al., 2015). Pokharel et al. (2017) demonstrated a strong inverse correlation between fecal glucocorticoid metabolites and BCS in free-ranging Asian elephants in India. Reports on the influence of stressful situations on zoo elephants' BCS is scarce. Hoby et al. (2015) documented the impact of living on a construction site on physical parameters in a group of female African elephants. Looking at the BCS graphs for these four elephants in the present study, a temporary decrease was evident in three of them (Fig. 6). It can be speculated whether the fourth female is a less fearful character and thus less vulnerable to disturbances than her counterparts. Another explanation might be her low social rank, which may make her feel less responsible for the safety of the group and thus less stressed. The negative impact on these elephants' physiology is confirmed by a similar pattern detected in further parameters (body weight, hormonal cycles, serum protein levels) (Hoby et al., 2015). As discussed by Hoby et al. (2015), it might not be ideal to keep elephants on a construction site if their level of stress leads to alterations in physical parameters. Visual BCS may be used as one of several parameters to evaluate chronic stress levels in elephants.

Transfers between facilities present another stressful situation for zoo elephants. However, they are temporarily restricted and inevitable for the breeding management of a zoo population. We found visible alterations in BCS graphs after transfer in two male Asian elephants (Fig. 6). While the adult male seemed to overcome the arrival in a breeding group quickly and gained condition continuously, the five-year-old male expressed a temporary decrease in BCS after being introduced into a bachelor group. Introduction of a young elephant into a new social environment can be considered very challenging for the individual and a temporary loss in condition is to be expected. The influence of various factors (e.g. age at time of transfer, diet, social environment, management) may be responsible for these BCS changes.

Overweight and obesity have been recently reported in North American as well as European zoo elephants (Morfeld et al., 2014; Morfeld et al., 2016; Schiffmann et al., 2018). An inappropriately energy-rich diet is considered one of the main causing factors (Hatt and Clauss, 2006). Nevertheless, only one study has confirmed the effect of diet adaptations on zoo elephant´s BCS (Carneiro et al., 2015). The latter report documented a significant decrease in body condition of two female Asian elephants three months after reducing dietary energy provision by >50% in a Brazilian zoo. Similar effects of diet adaptations on BCS have been reported in domestic mammals (ponies: Bruynsteen et al. (2015), dogs: Kealy et al. (2002) and rabbits: Prebble et al. (2015)) as well as zoo-kept baboons (Cabana et al., 2018). Our graphs for a collection keeping African (Fig. 8) and another one keeping Asian elephants (Fig. 9) demonstrate a decrease in BCS after a change in diet regimens. Although not quantified, the latter consisted of an increase in roughage while decreasing concentrates, and at the same time extending feeding enrichment. Being aware of the intense efforts of modern zoos to further improve their elephant husbandry and welfare, documentation of BCS approaching an ideal range might present a powerful confirmation for the actions taken.

(II) Data analysis European zoo elephant population regarding season and change over years

According to our findings European zoo elephants express no seasonal variation in BCS. This is in contrast to reports investigating free-ranging populations of both elephant species (Albl, 1971; De Klerk, 2009; Pokharel et al., 2017; Ramesh et al., 2011; Ranjeewa et al., 2018). In the latter, seasonal availability and quality of diet is considered the driving factor for changing physical condition in elephants. The majority of zoos across Europe provide a high-quality daily ration to their elephants independent of season, which might explain the stable condition in this population. It can be speculated whether a seasonal pattern regarding diet composition and energy content would be beneficial for zoo elephants. Although this approach might imitate the situation in the wild, this does not a priori mean an enhanced well-being for the animals (Veasey, 2018). Nevertheless, seasonal variation in diet could potentially reinforce favorable environment-induced mechanisms. If coupled with suggestions to consider elephants as long day breeders (Hufenus et al., 2018), an increase in BCS in the same time period as an increasing day length might boost reproduction. Targeting self-sustaining zoo elephant populations, further research in this aspect might be of special interest.

With respect to the significant adaptations of modern zoos in their elephant husbandry and management, meaningful improvements in welfare and healthcare are expected. Evaluation of an elephant´s physical condition functions as one prominent indicator of its shape. Thus, on a population-wide basis we expect these improvements in living conditions to lead to BCS closer to an ideal range. Considering the time span between 2000 and 2017, the graph for the Asian species meets these expectations, and in the African elephant a trend towards lower scores is detectable as well (Fig. 10). Observations of the population-wide change over the next decades will allow deeper insights into this correlation.

Conclusion

In this longitudinal description of BCS change over time in a zoo animal species, visual body condition scoring presented a practical tool. Patterns associated with incidents, age and management actions were detectable on the individual elephant basis as well as on a population-wide perspective. A more complete dataset might be achieved by archiving standardized photographs on a regular basis (e.g. quarterly). Nowadays available technology makes photographing as well as picture filing as easy as never before. To minimize additional workload for zoo staff, we propose the establishing and maintenance of an online database. Such a tool is available (exclusively for elephant-keeping facilities) in the form of an online BCS archive (https://www.elephants-of-europe.org/), where the first author collects and scores photographs of European zoo elephants. The archive is updated continuously and aims at an even more reliable documentation and interpretation of BCS over zoo elephant´s lifetime in the future. If proven useful in charismatic species such as elephants, similar systems might be introduced in further zoo animal species as well.

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Table 1 Results of General Linear Models linking the average body condition score (BCS) of a year to the year (2000-2017) and the average age, without (AR(0)) or with accounting for auto-regression with the previous (AR(1)) and with the two previous years (AR(2)).

	AR(0)		**AR(1)**			**AR(2)**			
Group	**Year**	**Age**	**Year**	**Age**	**BCS_{t-1}**	**Year**	**Age**	**BCS_{t-1}**	**BCS_{t-2}**
Both species & sexes	-0.054 (0.02)*	0.045 (0.03)	-0.051 (0.03)*	0.044 (0.03)	0.130 (0.25)	-0.048 (0.02)*	0.033 (0.03)	0.201 (0.24)	-0.361 (0.24)
E. max., both sexes	-0.059 (0.02)*	0.037 (0.03)	-0.059 (0.02)*	0.037 (0.03)	0.010 (0.24)	-0.068 (0.02)*	0.040 (0.03)	0.036 (0.24)	-0.324 (0.23)
E. max., females	-0.074 (0.03)*	0.048 (0.03)	-0.080 (0.03)*	0.049 (0.03)	-0.178 (0.24)	-0.081 (0.03)*	0.048 (0.03)	-0.189 (0.25)	-0.083 (0.25)
E. max., males	-0.021 (0.01)	0.005 (0.02)	-0.022 (0.01)	0.006 (0.02)	-0.048 (0.24)	-0.026 (0.02)	0.013 (0.02)	-0.081 (0.25)	-0.187 (0.26)
L. afr,, both sexes	0.018 (0.03)	-0.056 (0.07)	0.029 (0.04)	-0.071 (0.07)	0.182 (0.26)	0.035 (0.03)	-0.075 (0.05)	0.108 (0.20)	-0.436 (0.19)*
L. afr,, females	0.032 (0.03)	-0.076 (0.05)	0.038 (0.03)	-0.084 (0.05)	0.193 (0.24)	0.039 (0.02)	-0.081 (0.04)*	0.174 (0.19)	-0.530 (0.19)*
L. afr,, males	-0.066 (0.03)	0.054 (0.05)	-0.030 (0.03)	0.033 (0.04)	0.011 (0.20)	-0.028 (0.03)	0.010 (0.05)	0.001 (0.29)	-0.260 (0.22)

AR=auto-regression coefficient; parameters (slopes) are means with s.e. in parentheses; *=slope differs significantly from 0 (p<0.05)

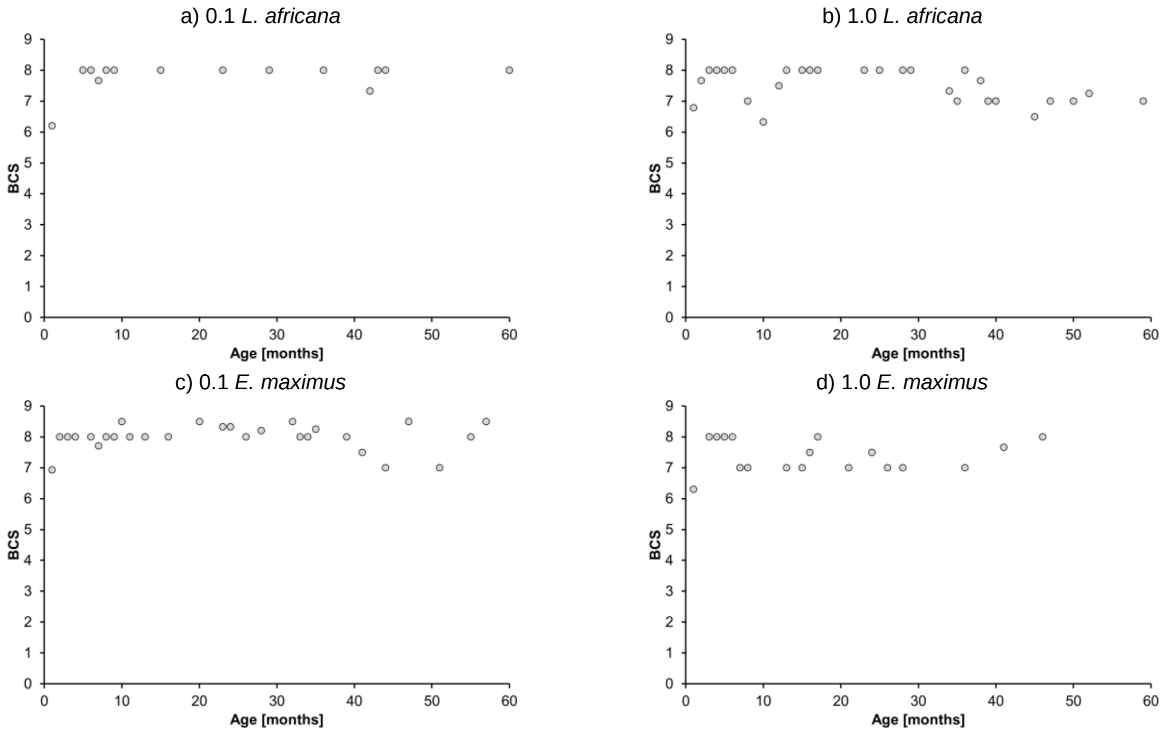

Figure 1 Change over time of body condition scores in individual zoo elephant calves during their first 5 years of life. The abbreviation 0.1 indicates female and 1.0 male individuals.

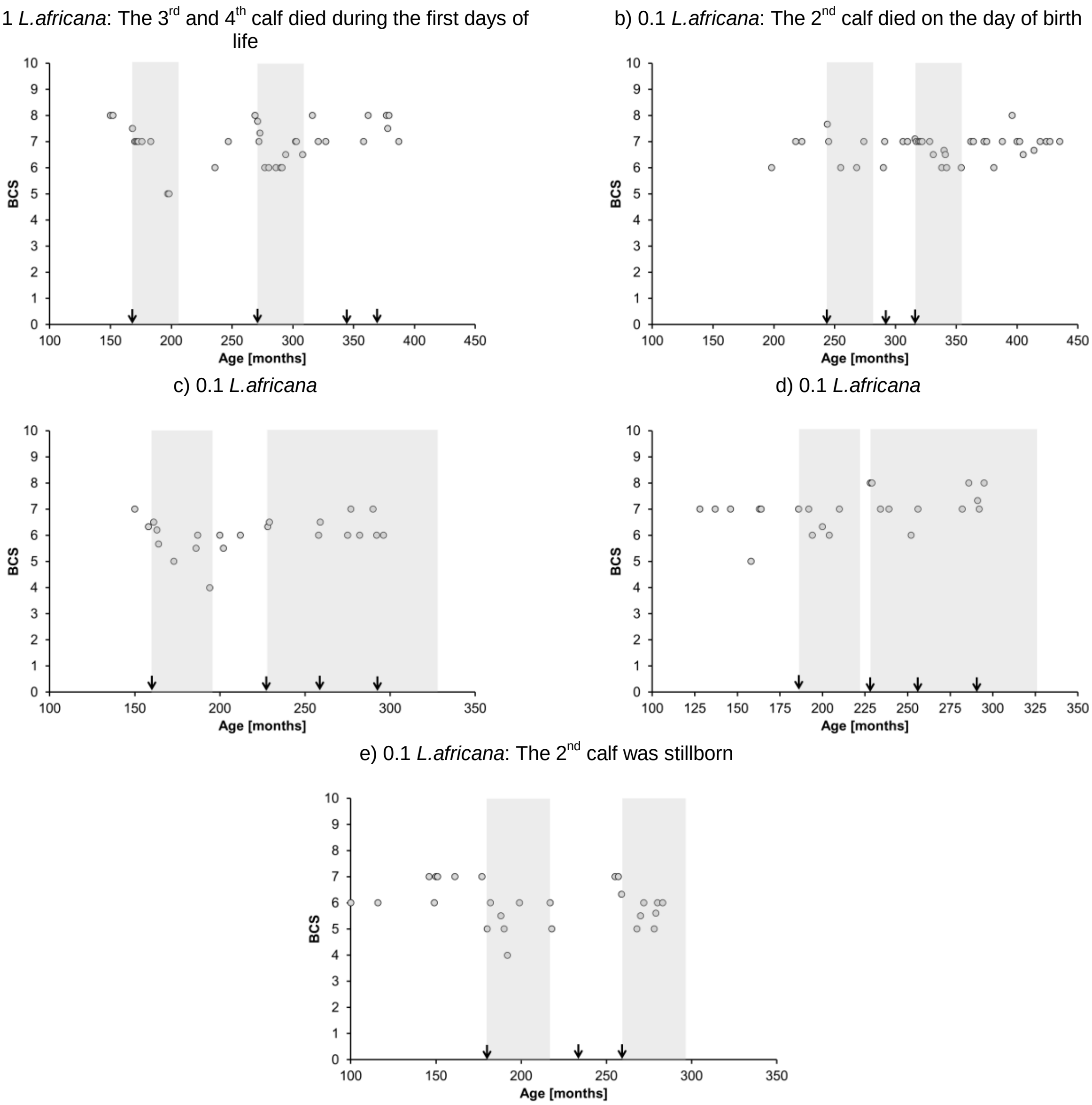

Figure 2 Change over time of body condition scores in breeding female African zoo elephants (black arrows indicate occurrence of a birth and grey shading the assumed duration of lactation (typically 36 months, but shorter in case of death of the neonate). The abbreviation 0.1 indicates female individuals.

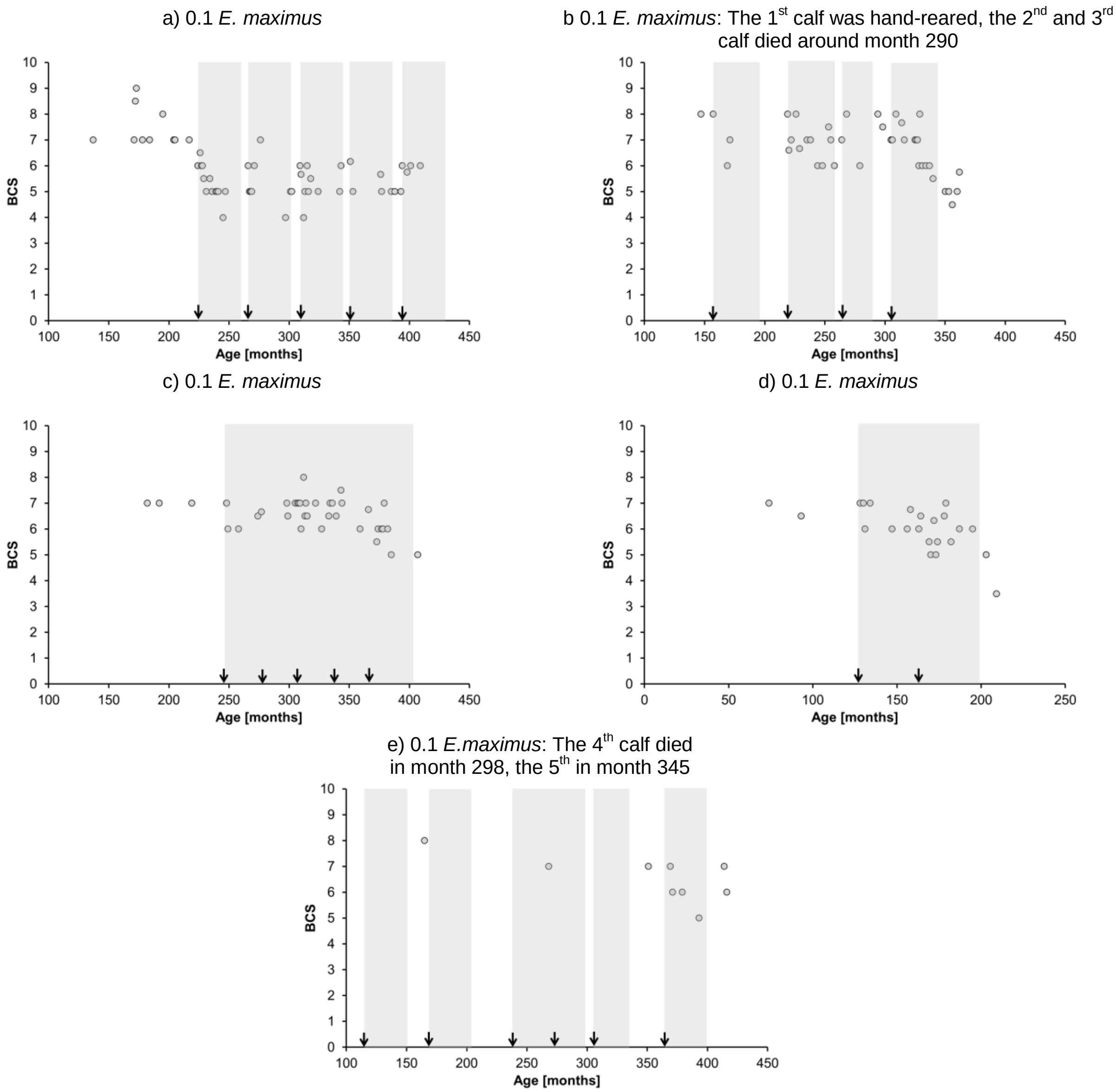

Figure 3 Change over time of body condition scores in breeding female Asian zoo elephants (black diamonds indicate occurrence of a birth and grey shading the assumed duration of lactation (typically 36 months, but shorter in case of death of the neonate). The abbreviation 0.1 indicates female individuals.

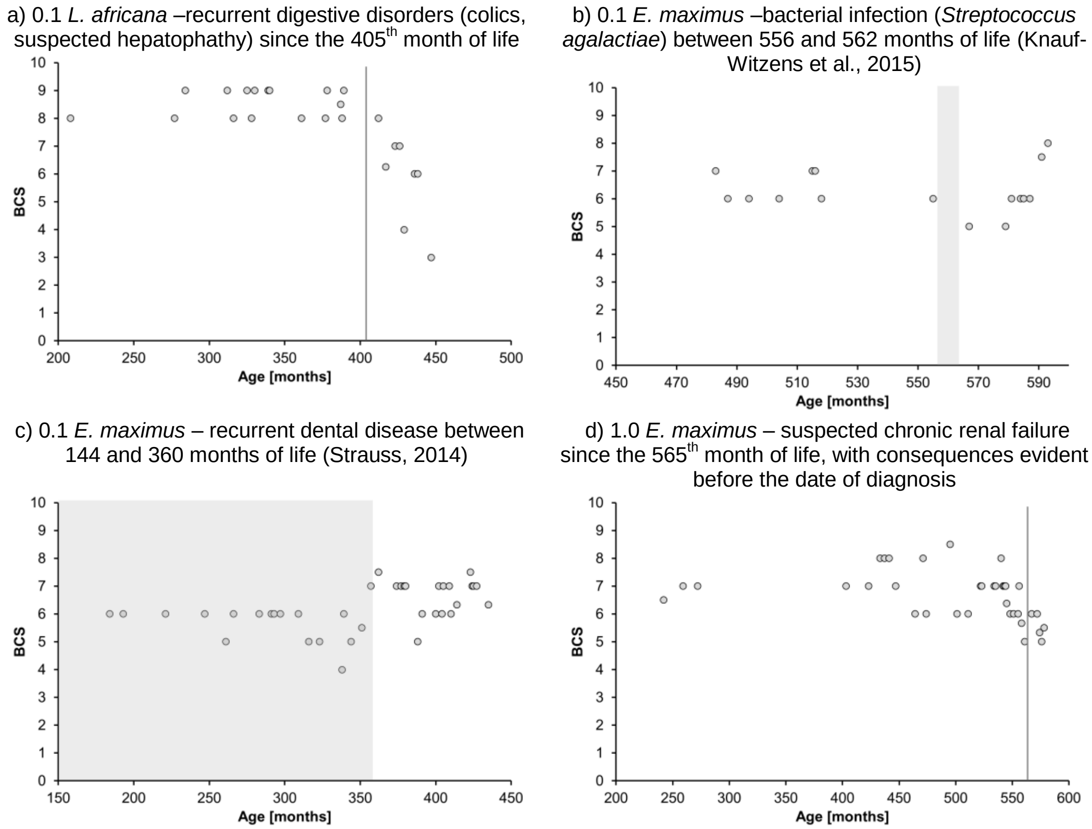

Figure 4 Change over time of body condition scores in zoo elephants during periods of disease (grey shading/vertical lines indicate the duration / beginning of the pathology, respectively). The abbreviation 0.1 indicates female and 1.0 male individuals.

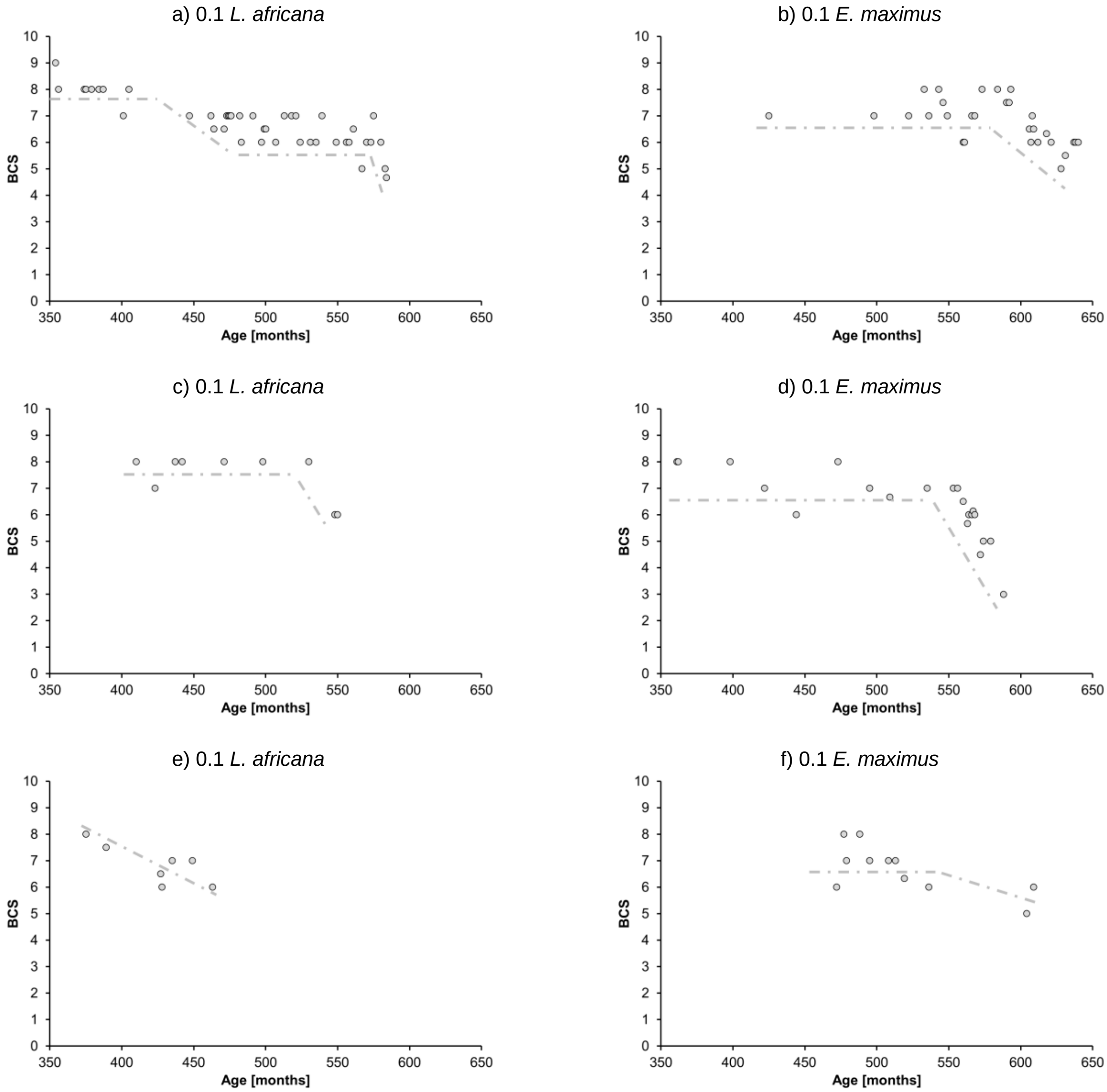

Figure 5 Change over time of body condition scores in aged zoo elephants (the dashed line visualizes the BCS change over time, but does not present a statistical trend line). The abbreviation 0.1 indicates female individuals.

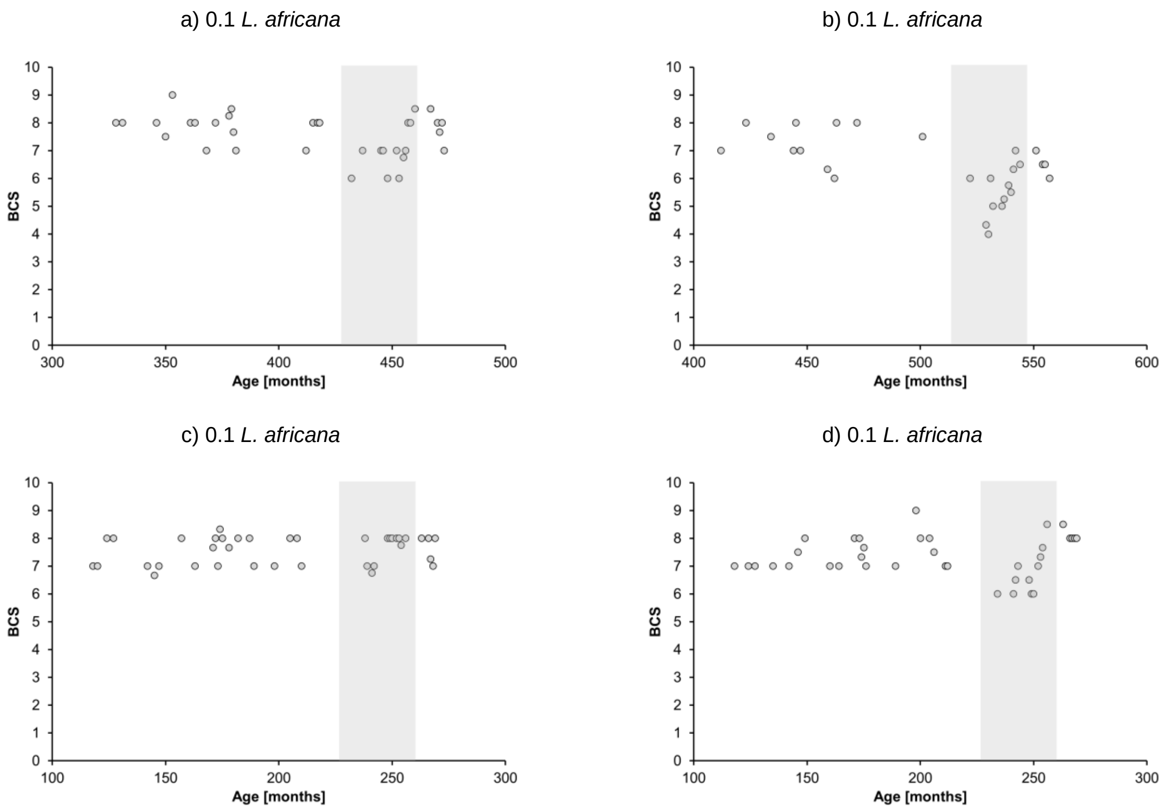

Figure 6 Change over time of body condition scores in a group of African elephants from a zoological institution during a stressful period through living on a construction site (grey shading indicates the duration of disturbances). The abbreviation 0.1 indicates female individuals.

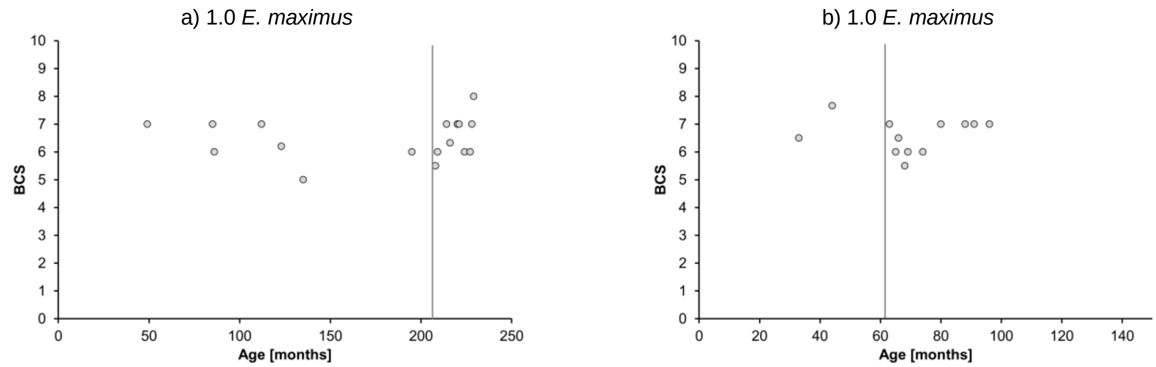

Figure 7 Change over time of body condition scores in two male Asian elephants transferred between two European facilities (vertical lines indicate the time of arrival at the new zoo). The abbreviation 1.0 indicates male individuals.

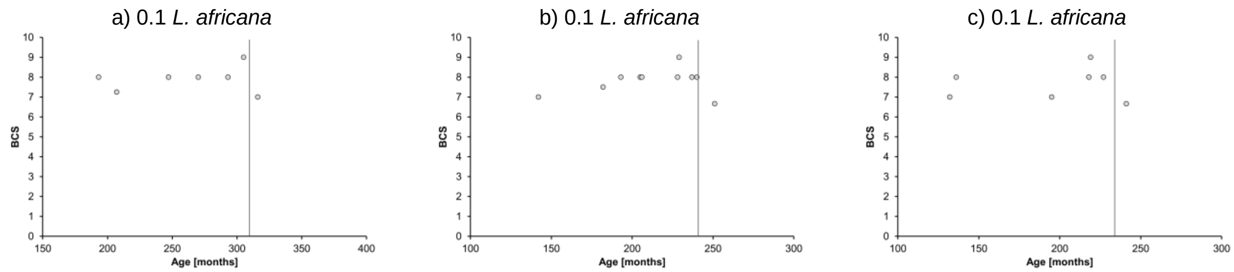

Figure 8 Change over time of body condition scores during diet adaptation in a female group of African zoo elephants (vertical lines indicate the implementation of the new feeding regimen). The abbreviation 0.1 indicates female individuals.

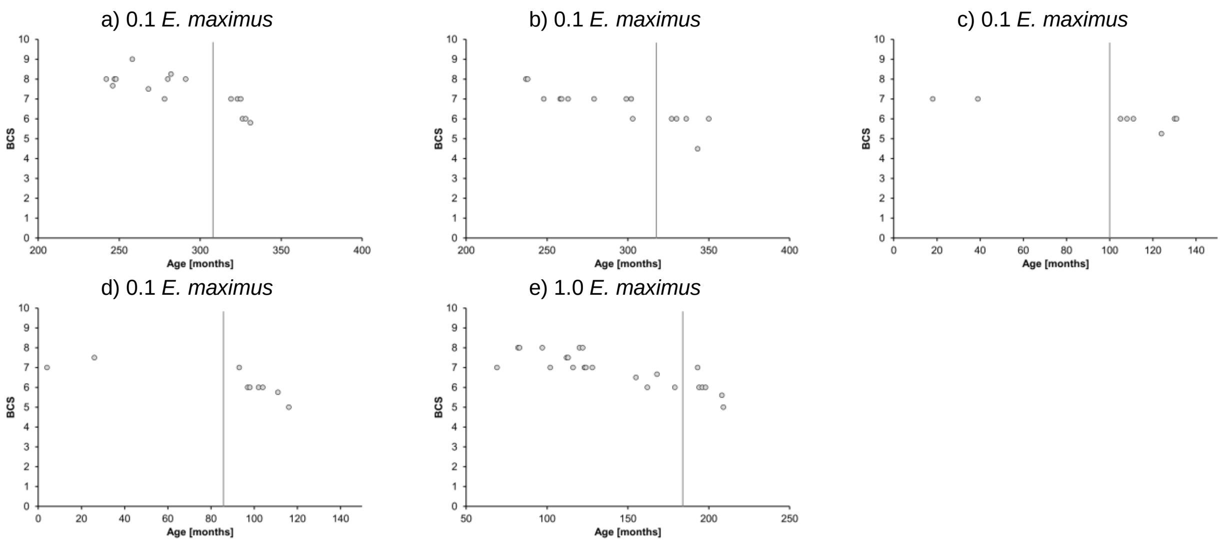

Figure 9 Change over time of body condition scores during diet adaptation in a breeding group of Asian zoo elephants (vertical lines indicate the implementation of the new feeding regimen). The abbreviation 0.1 indicates female and 1.0 male individuals.

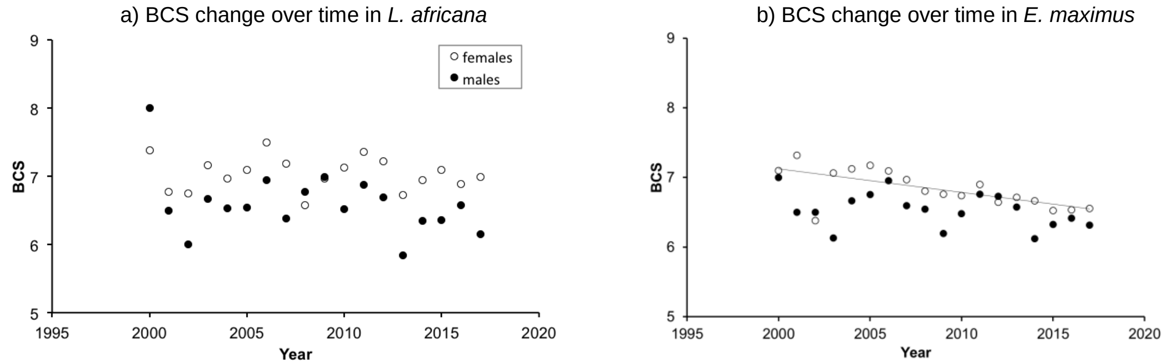

Figure 10 Population-wide change of age and body condition scores in European zoo elephants over the course of 18 years (2000-2017). In total annual scores for 470 females and 101 males of *L. africana* (a) and 917 females and 167 males of *E. maximus* (b) were considered. Only the decline in BCS over time in Asian females was significant (cf. Table 1).

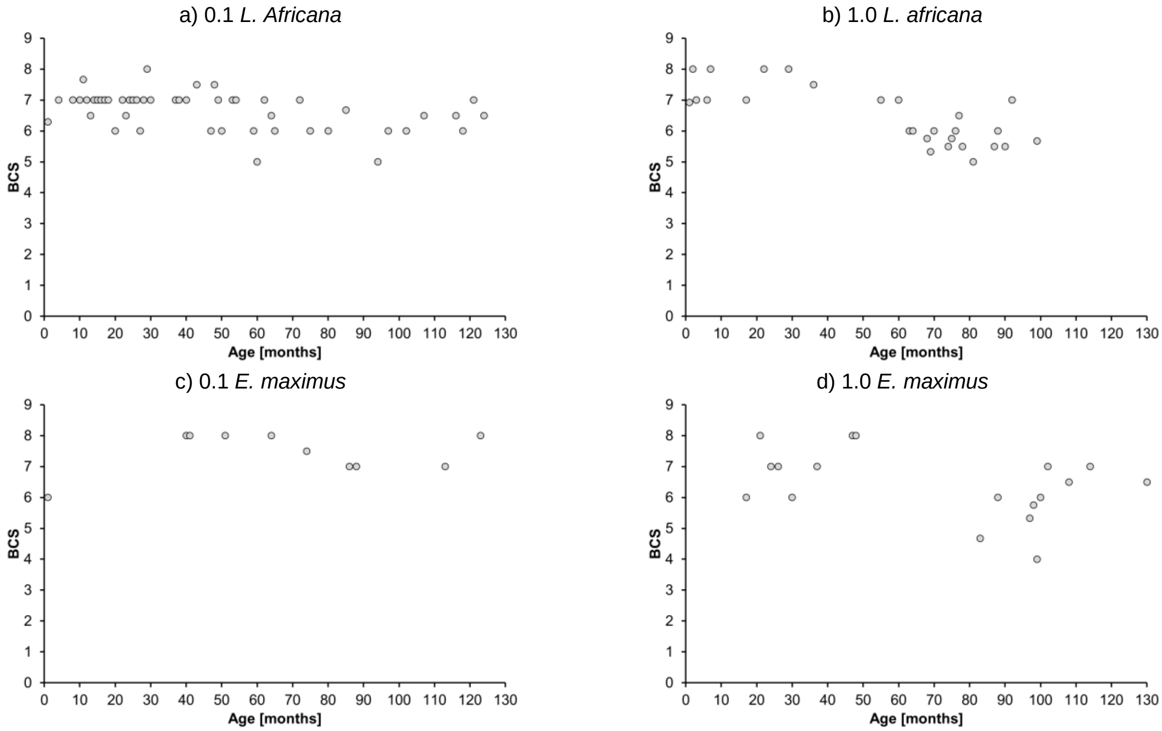

Figure 11 Change over time of body condition scores in young sub-adult zoo elephants between 5 and 10 years of age. The abbreviation 0.1 indicates female and 1.0 male individuals.

Weigh and see – Body mass recordings versus body condition scoring (BCS) in zoo elephants (*Loxodonta africana* and *Elephas maximus*)

Christian Schiffmann, Jean-Michel Hatt, Stefan Hoby, Daryl Codron, Marcus Clauss

In preparation for submission

Neben dem Body Condition Scoring stellt das Wiegen eine weitere Option zum Monitoring der physischen Verfassung von Zooelefanten dar. Ob und wie Körpermasse und BCS korrelieren sowie die Gewichtsentwicklung im Laufe des Lebens, wurde an gesammelten Daten der Europäischen Zooelefantenpopulation untersucht.

Weigh and see – Body mass recordings versus body condition scoring (BCS) in zoo elephants (*Loxodonta africana* and *Elephas maximus*)

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Abstract

Regular body mass monitoring plays a key role in preventative health care of zoo animals. In some species including African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*), the process of weighing can be challenging and alternative methods such as visual body condition scoring (BCS) have been developed. We investigated the temporal development of both parameters regarding correlation patterns and their sensitivity in dependence of an elephant´s life stage. While weighing seems more sensitive in calves and juveniles under the age of 8 years, both methods are considered equal in adult elephants. In elephants of advanced age (> 40 years), BCS might be more sensitive in assessing the physical status. Independent of species and sex, juvenile zoo elephants grow in body mass nearly linearly with age, and reach a higher body mass at an earlier age compared to free-ranging and semi-captive populations in the countries of origin; non-breeder status seems to be associated with a higher body mass. Growth rates drastically decline and even become negative between 150 and 200 months of life. After this temporary drop, body mass cycles with peaks at intervals around 100 months in both breeders and non-breeders, and increases of variable rates occur even after 40 years of age. We hypothesize molar replacement as underlying cause for this pattern and recommend consideration of a zoo elephant´s molar state when assessing its current body mass and body condition. Regular body mass recording in zoo elephants is strongly recommended in order to enhance our knowledge on body mass development and allow the formulation of practical recommendations. BCS presents a valuable and simple tool for complementary monitoring of an elephant´s condition, especially in adult and geriatric individuals.

Key words: zoo elephant, BCS, body mass development, molar replacement

Introduction

Correlation between BCS and body mass

Body condition and body mass monitoring are considered integral parts of preventative health care in zoo animals - especially in species tending to become overweight or even obese under conditions of captivity. The African and Asian elephant represent such species (Hatt and Clauss 2006; Morfeld et al. 2014; Morfeld et al. 2016; Schiffmann et al. subm.). Due to their sheer size and body mass, weighing is a challenging task for elephant-keeping facilities (Wijeyamohan et al. 2010). Thus, alternative monitoring methods like visual body condition scoring (BCS) or body mass calculation out of morphometric measurements have been developed and validated to varying degrees (reviewed in Chapman et al. (2016) and Schiffmann et al. (2017)). Probably due to these challenges, comprehensive body mass data over the course of time for individual zoo elephants are scarce and typically limited to narrow periods of an elephant´s life (Fischer et al. 1993; Lang 1994; Schwammer et al. 2001; Miller and Andrews 2013). According to our knowledge, investigations on the correlation of results of weighing, which is considered the gold standard for body mass monitoring (Chapman et al. 2016), and BCS have not been conducted in a comprehensive sample of zoo elephants yet. It is the objective of this report to assess the relationship of these methods and to derive recommendations regarding their applicability with respect to an elephant´s life stage.

Body mass development

Additionally, the compilation of mean growth curves for elephants provides insights into body mass development and influencing factors under zoo conditions. Literature data on growth rates exists for captive and semi-captive Asian elephants in their range countries as well as for captive and free-ranging African elephants, although most of these data are restricted to morphometric (shoulder height, thorax circumference, foot length and/or circumference) or indirect (foot print length, dung bolus size) measurements (McCullagh 1969; Sukumar et al. 1988; Lindeque and van Jaarsveld 1993; Lee and Moss 1995; Weihs et al. 2001; Reilly 2002; Morgan and Lee 2003; Shrader et al. 2006). A few reports on body mass development in elephants exist, often with restricted sample sizes (Laws 1966; Krumrey and Buss 1968; Kurt and Nettasinghe 1968; Hanks 1969; Hanks 1972; Sukumar et al. 1988; Fischer et al. 1993; Lang 1994; Kurt and Kumarasinghe 1998; Schwammer et al. 2001; Miller and Andrews 2013; Walker and Schlegel 2013). We compare the body mass growth curves we obtained from current European zoos to these literature data.

Material and methods

Within the scope of the population-wide BCS assessment in European zoo elephants (Schiffmann et al. subm.), additionally body mass data were collected wherever available. Data collection was conducted on site as well as remotely by mail contact, and is described in a previous report together with the applied method for body condition scoring (Schiffmann et al. subm.). To facilitate comparability of body mass development between individuals, each body mass was ascribed to age measured in months of life of the assessed elephant. Where more than one body mass per month of life was available, we calculated the mean. Subsequently we plotted the body masses against the months of life for each elephant. Where BCS data for an individual were available as well, we linked them to age in the same manner as the body masses and added them to the graphs. By checking the resulting multitude of graphs for reoccurring patterns, we selected individual elephants for further display and interpretation. We tested for nonparametric correlations between age, body mass and BCS. Statistical procedures were performed in SPSS 23.0.0 (IBM Corp., Armonk, NY), with the significance level set to 0.05.

Correlation between BCS and body mass

For the determination of a potential correlation between body mass and BCS, we considered only elephants for which at least 10 records of body mass and BCS values were available within the same time period. Besides statistically testing for nonparametric correlation between body mass and BCS, we restricted further interpretations to a descriptive approach due to data format and sample size.

Body mass development

We visualized body mass development separately for species and sex by plotting the population-wide mean body mass per month of life against month of life. To increase stability of our results, only months with body mass records of at least three individual elephants were considered. During periods with rare body mass data (e.g. in African females before 50 and after 380 months of life), we took into account calculated mean body masses if at least three body masses (from one or various individuals) per three consecutive months were available. The different nature of these data is indicated in the corresponding graphs. To investigate the influence of reproductive activity on body mass development in female elephants, we defined all females which experienced at least one live birth and rearing of a calf during their lifetime as “breeders”. In contrast, we categorized all females over the age of 10 years without any live birth as “non-breeders”.

Literature research on reported growth curves (especially regarding body mass) provided data for comparison. Where data were not available as mean body mass per month, the mean was calculated out of the given range (e.g. Fischer et al. (1993)). Furthermore, body mass grow curves were extracted from published graphs by the use of an online tool (https://automeris.io/WebPlotDigitizer/). This method allowed the compilation and comparison of various body mass development curves in one single graph.

Results

In total we collected body mass data of 41 African (27 females, 14 males) and 100 Asian elephants (70 females, 30 males). In both species female body mass data were much more comprehensive than records for males and cover a wider period of life (Fig. 1). Body mass data for African and Asian males exceeding 200 months of life were rarely reported. The same was the case for female African elephants over the age of 400 months.

Testing for nonparametric correlation between BCS and body mass revealed several statistically significant correlations, although restricted to specific sex/age classes (Tab. 1). There was generally a significant positive correlation between age and body mass in all elephants considered, regardless of whether all age groups, or only juveniles < 60 months, or adults > 60 months were considered. Only in elephants exceeding 360 months this correlation was no longer significant. In Asian males over the age of 40 years, a negative correlation between age and body mass became significant. By contrast, age was negatively related to BCS across all elephants, an effect mainly due to older animals and not present in the age class below 60 months of life. However, apart from significant correlations for elephants > 60 months of age, the effect was not generally evident when older age classes were considered. Correspondingly, there was no clear universal pattern in the relationship of body mass and BCS. In young growing elephants, there were positive correlations, even if the graphs (Fig. 2) rather show a picture of increasing mass at stagnating BCS. In older animals, there was a positive correlation for African females and Asian males exceeding 360 months of life, supporting the impression from graphs (Fig. 3) that in this age group, body mass and BCS often decreased in parallel. Furthermore, data collection and preparation resulted in 14 graphs for *L. africana* (10 females, 4 males) and 27 graphs for *E. maximus* (17 females, 10 males) fulfilling our selection criterion of at least 10 body mass and BCS records. We found different reoccurring correlation patterns between BCS and body mass development, depending on an elephant´s life stage. In calves and juveniles under the age of 8 years, body mass seems to increase in a linear fashion while BCS remains more or less stable on the score level 6-8/10 (Fig. 2 and Fig. S1 in supporting material). This pattern occurred consistently in 20 out of 21 elephants with sufficient data to be included. In contrast, BCS and body mass data showed a parallel development in adult elephants exceeding 20 years of age (Fig. 3 and Fig. S2 in supporting material). This pattern occurred consistently in 15 out of 17 elephants with sufficient data during this period of life. The transition between these two life stages therefore is of special interest, and our data collection provided four graphs (one for each species and sex) covering this period between 8 and 20 years of life (Fig. 4). The corresponding examples demonstrated unexceptionally an interruption of the previous body mass gaining rate. At the same time BCS showed a trend to decrease in three out of four individuals during this period (Fig. 4).

Literature research provided in total 18 curves demonstrating body mass growth in elephants, 6 for the African and 12 for the Asian species. In the African elephant 4 out of 6 graphs are based on data for free-ranging populations while the remaining two contain mixed data from free-ranging and captive individuals across Africa (Fig. 5a). Graphs for both sexes exist for this species. For zoo-kept African elephants only growth curves covering very short sections of their lifetime could be found in the literature and were not considered here (Lang 1980; Miller and Andrews 2013). In the Asian elephant 9 out of 12 graphs are based on data from semi-captive or captive populations in their countries of origin and obtain graphs for both sexes (Fig. 5b). The remaining two graphs show body mass development for female zoo elephants in one North American zoo respectively four facilities in Europe (Fig. 6a). No body mass growth curve for zoo-kept Asian elephant males seems to exist.

Discussion

With respect to the inherent subjectivity of visual body condition scoring, we tried to minimize this by the restriction to one single examiner and a strict scoring protocol (see method section). Moreover, the results from our previous study support the repeatability of the applied scoring method (Schiffmann et al. subm.). Our retrospective approach for data collection will never deliver ideal completeness for analysis and interpretation. Thus, it seems reasonable to assume that further patterns and stronger evidence might exist if data basis would have been more complete. Nevertheless, the collated data revealed insights into the correlation between BCS and body mass monitoring and its dependence of an elephant´s life stage. Extensive body mass documentation in several facilities with successful breeding allowed the demonstration of accurate body mass curves during the first years of life (Fig. 1). Unfortunately, data richness decreased with growing age, most likely due to the technical difficulty of weighing larger individuals, leaving gaps in our knowledge regarding this period of life. These gaps are more extended in the African species (Fig. 1), which might be due to the different demography of both populations (Schwammer and Fruehwirth 2016; van Wees and Damen 2016). The amount of available pictorial data and body mass records varied significantly between facilities. Thus, our descriptions and interpretations are biased towards elephants/institutions with more extensive documentation especially regarding regular body mass recordings. We cannot exclude that this circumstance led to the over- or underestimation of certain aspects. Therefore, our conclusions might not be considered invariably representative for the entire European zoo population.

Correlation between BCS and body mass

A positive correlation between BCS and body mass has been reported in armadillos (Clark et al. 2016), cheetah (Reppert et al. 2011) and the Asian elephant (Wijeyamohan et al. 2015). In cheetah and elephants this finding is restricted to adults or individuals of the same height (Reppert et al. 2011; Wijeyamohan et al. 2015). In growing calves with continuous body mass gain, BCS is not supposed to increase in parallel. Additionally, the different methodology might cause variable results. While weighing does not differentiate between the loss/gain of musculature and subcutaneous fat, these features are considered in BCS. Thus, if an elephant gains muscle mass while losing subcutaneous fat, his body mass may remain stable although his BCS will decrease. This complexity presents an explanation for the lacking of a general pattern and partially contradicting correlations between BCS and body mass in different sex/age classes (Tab. 1). A more consistent correlation might be detectable by putting body mass in relation to another morphometric measurement, as has been shown in several wildlife species including Asian elephants (Owen 1981; Stirling et al. 2008; Clements and Sanchez 2015; Wijeyamohan et al. 2015; Heidegger et al. 2016).

The descriptive evaluation of BCS vs. body mass graphs in single individuals leads to the assumption that sensitivity of visual body condition scoring might vary during a zoo elephant´s life (Fig. 2-4). This would be in contrast to Wijeyamohan et al. (2015) who declared the visual approach as valid for elephants independent of size and age class. Although it seems reasonable to assume a stable condition in growing elephants provided optimal diet and care in a zoo setting, body mass might be much more sensitive to inadequacies during this period. In adult zoo elephants, we often found roughly similar patterns of body mass and BCS development. Thus acceptable reliability and sensitivity of both methods is assumed during this period of life. In a previous report, we found decreasing BCS in 24 out of 38 zoo elephants over the age of 40 years (Schiffmann et al. in prep.). Results of our statistical analysis do not confirm a similar pattern in body mass development of 27 zoo elephants (Tab. 1). The plots of the available data reveal body mass gain even after the age of 45 years (Fig. 1). Thus, it can be hypothesized whether BCS might be more sensitive in determining physical condition in aged elephants compared to body mass. In the latter, a loss in physical condition might be outweighed by growth in height until late in an elephant´s lifetime (Haynes 2008). Again, putting body mass in relation to further morphometric measurements (e.g. shoulder height) might provide deeper insights into this aspect.

Body mass development

With respect to growth in height until late in an elephants life (Haynes 2008), a corresponding body mass gain is expected. Nonparametric statistical analysis of our data confirms this assumption and shows positive correlation pattern between age and body mass, with negative relationships occurring exceptionally in age classes exceeding 360 months of life (Tab. 1). Furthermore body mass development seems to vary between different age classes. It is unclear whether scarcity of available body mass data for zoo elephants over the age of 150 months (especially males of both species) is caused by a reduced cooperation or inappropriate scales regarding their sheer size. Collected data originate from facilities with different management systems (protected and free contact). Thus, regular weighing and data recording has proven feasible independent of management system and is strongly recommended for each facility with a scale on site. When comparing body mass development of free-ranging and (semi-)captive elephant populations, the following limitations should be kept in mind. Although, natural growth in free-ranging African elephants has been studied intensively, it was mainly focused on indirect and morphometric measurements (McCullagh 1969; Lee and Moss 1995; Morgan and Lee 2003; Shrader et al. 2006). Only a few reports on directly measured body mass data exist (Johnson and Buss 1965; Laws 1966; Krumrey and Buss 1968; Hanks 1969; Hanks 1972). Due to the fact that their data originate from culling operations, they contain several limitations. Age estimation was based on previously reported protocols which might vary in accuracy depending on the investigated population as emphasized by Lindeque and van Jaarsveld (1993). Moreover, data for elephant calves and juveniles under the age of 10 years are very sparse (Laws 1966; Krumrey and Buss 1968; Hanks 1969; Hanks 1972). In the Asian species the majority of data originate (semi-)captive populations in their countries of origin (Fig. 5b), with presumably heavily varying living conditions as well as methods of age determination and body mass recording.

Calves and Juveniles

We demonstrate a nearly linear body mass growth in European zoo elephants until month 150 of life independent of sex and species (Fig.

1). This pattern is in accordance with findings from the literature for the African (Lang 1980; Miller and Andrews 2013 and Fig. 6b + c) as well as the Asian species (Fig. 6a + d). The incline of our curves for the European zoo population is distinctively steeper compared to data from free-ranging and (semi-)captive populations in the countries of origin (Fig. 6). This pattern is valid independent of species and sex and leads to up to 150% higher body mass at an earlier point of life in European zoo elephants. Compared to data collected for Asian females living in four European zoos by Kurt and Kumarasinghe (1998), the incline until month 150 of life looks similar (Fig. 6a). In contrast, Weihs et al. (2001) found slightly retarded growth patterns in captive juvenile males compared to free-ranging ones. This pattern might be caused by exclusively focusing on orphans, which leads to the conclusion that an intact mother-offspring relation is critical for normal body growth in young and juvenile Asian elephants (Weihs et al. 2001). Considering the growing number of family units living in European facilities (Schwammer and Fruehwirth 2016; van Wees and Damen 2016), this aspect might be of minor relevance for the population investigated here. Our finding that individuals of both elephant species living in European zoos become heavier compared to elephants living under more extensive conditions is in perfect accordance with the literature (Hanks 1972; Lindeque and van Jaarsveld 1993; Walker and Schlegel 2013) and a survey in 19 European and North American zoos, which found female elephants of both species to be 600-700 kg heavier compared to benchmarks for their free-ranging counterparts (Ange et al. 2001). This difference can be explained by the continuous provision of an unnaturally energy-rich diet and reduced physical activity under zoo conditions (Hatt and Clauss 2006). The positive correlation between diet and growth rate is well-known in farm animals (Borton et al. 2005; Pla 2008; Blanco et al. 2014), has been detected in reptiles (Ritz et al. 2010) as well as nutria (Glogowski et al. in prep.), and might exist in further wildlife species. Moreover, dependence of height growth from caloric intake has been demonstrated in humans (Fomon et al. 1969; Berkey et al. 2000). A deviation from the linear body mass gain curve in calves and juveniles might indicate inadequacies or disorders in an individual elephant. Construction of percentile curves might serve as an objective and clear guideline for breeding facilities to monitor the development of an elephant calf. According to Miller and Andrews (2013) and Kiso et al. (2017) morbidity of physical disorders is elevated during the first years of an elephant´s life; therefore, reliable monitoring tools are of outmost importance in this period.

Adult females

Available data of direct body mass measurements for free-ranging African females indicate a significant decrease in growth rate after the age of 20 years (Fig. 5a). Our data reveal a reduction in body mass growth rates between month 150 and 200 of life (Fig. 6b). Population-wide data (Fig. 1) as well as individual curves (Fig. 4) corroborate the drop in body mass gain and even body mass loss in female zoo elephants after the age of 20 years reported by Walker and Schlegel (2013) and are discussed extensively further down below. As mentioned before, female Asian zoo elephants reach their maximum body mass earlier and on a higher level compared to their semi-captive and captive counterparts in countries of origin, although body mass curves of both populations do converge when age exceeds 45 years (Kurt and Kumarasinghe 1998) (Fig. 6a). In contrast to the zoo data compiled by Kurt and Kumarasinghe (1998), body masses of female Asian elephants investigated here do not reach their maximum between the age of 25 and 30 years. They do rather increase even after the elephants exceed 45 years (Fig. 6a). Although restricted by the small sample size, body mass data reported by Fischer et al. (1993) for female Asian elephants from one North American zoo are on a lower level compared to our current study (Fig. 6a). This difference might be explained by varying management systems in Europe and North America. Unfortunately, no comprehensive body mass data from the North American zoo elephant population have been published yet, making real comparisons impossible. Considering the fact that BCS has been recently shown to be significantly higher in North American zoo elephants (Schiffmann et al.

subm.), we would not expect them to be lighter in a population-wide perspective. Breeding females of both species showed lower body mass than non-breeders (Fig. 7) which is in accordance to the reported correlation of reproductive problems and obesity in captive African females (Freeman et al. 2009), although current research found no correlation between fat mass and cycling activity in African females living in North American zoos (Chusyd et al. 2018). Thus, further investigation into the relationship of body mass and reproductive success in captive female elephants is strongly recommended.

Adult males

Our data reveal a reduction in body mass growth rates between month 150 and 200 of life, although data for African males are limited to individual growth curves (Fig. 1 + 4). Compared to free-ranging, semi-captive and captive populations in their range countries, African and Asian males in European zoos seem to become heavier at an earlier point in their life (Fig. 6c + d). This means that zoo-kept males grow at an increased rate. Whether the growth curves become similar after the age of 40 years, as it is the case in females, remains speculative due to a lack of data for zoo-kept males (Fig. 1). The increased body mass growth rate under zoo conditions corroborates the assumption (Kurt and Nettasinghe 1968) respectively findings (Kurt and Kumarasinghe 1998) for the Asian species in previous reports. In contrast, Sukumar et al. (1988) who measured shoulder height and body mass of captive Asian elephants in an Indian sanctuary, did not find any difference in growth rates between captive and free-ranging elephants, but presumed free-ranging males to become taller than captive-born ones. Due to that fact, they supposed free-ranging males to become heavier while they did not expect a difference in body mass curves of captive and free-ranging females (Fig. 5b). If the assumption by Sukumar et al. (1988) should be correct this might refer to a deficient diet quality in sanctuary conditions, although this remains speculative.

Temporary body mass drop

Our data document a distinct body mass drop between month 150 and 200 of life (Fig. 1). This temporary body mass loss is evident in population-wide as well as individual growth curves and independent of species. In females this characteristic pattern is more distinct, probably due to the sparsity in body mass data for males exceeding 150 months of life (Fig. 1). In a group of six female African elephants in a North American zoo a temporary body mass loss has been reported for the period between 17 and 23 years of age by Walker and Schlegel (2013). This body mass loss varied in its extent between the individual elephants and due to the absence of subsequent data, no information on the duration of this pattern is provided (Walker and Schlegel 2013). Furthermore, the report on free-ranging female African elephants by Hanks (1972) contains some indicators of a potential body mass drop after the age of 20 years. Unfortunately, these data are incomplete in density and not collected longitudinally, thus restricting further interpretations. Although it can be speculated that body mass data from one single North American zoo (Fischer et al. 1993) support the temporary body mass drop reported here, the pattern is lacking in further previous reports on Asian elephant body mass development (Fig. 1 + 6a). This might be due to the sparsity of comprehensive data over the course of an elephant´s life. It can be speculated whether entering reproductive activity with demanding lactation periods might lead to the body mass drop, but the seemingly parallel development of breeding and non-breeding females provides no support for this hypothesis (Fig. 7). Additionally available data refer to a similar drop in growth rates in male elephants (Fig. 1). Future data collection will elucidate whether this temporal body mass loss does really occur in a similar extent in male elephants. While such a pattern of a peak in body mass with a subsequent drop after the cessation of growth is known in many bird species (Ricklefs 1968), it is not common in mammals.

Cyclicity

After the aforementioned drop, body mass seems to cycle at an interval of around 100 months (Fig. 7). This pattern is obvious in females of both species but not in males, potentially due to incomplete data in the latter (Fig. 1). Due to its length and the occurrence in non-breeding females (Fig. 7), we do not believe this cyclicity to be caused by reproductive activity. We rather hypothesize molar development with continuous molar replacement every 10-15 years to have an impact on body mass patterns as discussed in extent elsewhere (hier Zitat des bodymassandmolarprogression-manuskripts). Assuming this hypothesis to be correct would mean that zoo elephants´ body condition does vary with their molar state, and that zoo managers should keep such a potential pattern in mind when assessing an individual elephant's body mass. Thus, when targeting an ideal physical condition of zoo elephants at any point of their life, this aspect should be considered in practice. Further investigation regarding differences of molar attrition and replacement, and possibly an accompanying monitoring of the lifetime chewing efficiency via faecal particle size (Clauss et al. 2015), between both elephant species as well as zoo versus free-ranging conditions are needed to reliably examine and refine our hypothesis.

Conclusions

1. BCS vs. weighing: A more accurate assessment regarding which approach should be preferred needs further investigation. In our opinion the combination of both methods might be the best option due to their complementary peculiarities. While the acquisition of an appropriate scale means a financial burden, regular taking and storage of photographs for BCS might be feasible for each facility in short-term. Furthermore, the archiving and scoring process might be facilitated by the development and maintenance of an external online archive.

2. Body mass development: Independent of species and sex zoo elephants reach higher body masses at an earlier point of their lifetime compared to free-ranging or (semi-)captive elephants in the countries of origin. This pattern is presumably caused by the continuous provision of an energy-rich diet in European zoos.

3. Body mass and breeding activity: Breeding females of the European zoo population expressed distinctly lower body masses compared to their non-breeding counterparts. Targeting a self-sustaining captive population requires ideal reproductive performance and further investigation into its correlation with body mass is strongly recommended.

4. Body mass drop/cyclicity: We report a significant body mass drop in zoo elephants between month of life 150 and 200 as well as a consequent cyclicity with peak body masses at intervals of around 100 months. We hypothesize this pattern to be caused by molar replacement, a varying grinding surface and consequent changes in the effectiveness of mastication.

5. To gain deeper insights into body mass development of zoo elephants especially in adults, regular data collection and storage is strongly recommended. Subsequent publication of such data might provide valuable guidelines for elephant-keeping institutions as emphasized by Fischer et al. (1993). They will not only serve for comparisons with the situation in the wild, but provide guidelines for normal body mass development under the conditions of captivity. Moreover comprehensive data will allow the investigation of correlation patterns with further medical parameters (e.g. hematology, hormone analysis) and disorders (e.g. reproductive abnormalities, musculoskeletal disorders, foot pathologies). Research in the latter might facilitate an objective definition of body mass ranges for “normal weight”, “overweight” or “obesity” in relation to an elephant´s life stage.

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Table 1 Nonparametric correlations between age, body mass (BM) and body condition score (BCS). Significant correlations are written in bold with the significance level set to 0.05

	n (age range in months)	Age-BM	Age-BCS	BM-BCS
All elephants	499 (1-763)	**ρ = 0.89** **P < 0.001**	**ρ = -0.12** **P = 0.006**	ρ = -0.06 P = 0.165
***E. maximus* - females**	180 (1-763)	**ρ = 0.95** **P < 0.001**	**ρ = -0.19** **P = 0.010**	ρ = -0.08 P = 0.300
***E. maximus* - males**	98 (1-561)	**ρ = 0.98** **P < 0.001**	**ρ = -0.37** **P < 0.001**	**ρ = -0.33** **P = 0.001**
***L. africana* - females**	157 (1-536)	**ρ = 0.83** **P < 0.001**	**ρ = -0.19** **P = 0.017**	ρ = 0.16 P = 0.053
***L. africana* - males**	64 (1-334)	**ρ = 0.99** **P < 0.001**	**ρ = -0.26** **P = 0.042**	ρ = -0.22 P = 0.075
Elephants up to 60 months	132 (1-60)	**ρ = 0.93** **P < 0.001**	ρ = 0.139 P = 0.112	**ρ = 0.28** **P = 0.001**
***E. maximus* - females**	68 (1-59)	**ρ = 0.93** **P < 0.001**	ρ = 0.22 P = 0.073	**ρ = 0.42** **P < 0.001**
***E. maximus* - males**	23 (1-60)	**ρ = 0.92** **P < 0.001**	ρ = 0.15 P = 0.486	ρ = 0.15 P = 0.503
***L. africana* - females**	14 (1-60)	**ρ = 0.99** **P < 0.001**	**ρ = 0.66** **P = 0.011**	**ρ = 0.64** **P = 0.014**
***L. africana* - males**	27 (1-53)	**ρ = 0.99** **P < 0.001**	ρ = 0.02 P = 0.925	ρ = 0.08 P = 0.698
Elephants older than 60 months	367 (61-763)	**ρ = 0.73** **P < 0.001**	ρ = -0.09 P = 0.088	ρ = 0.004 P = 0.936
***E. maximus* - females**	112 (61-763)	**ρ = 0.81** **P < 0.001**	**ρ = -0.36** **P < 0.001**	ρ = -0.14 P = 0.133
***E. maximus* - males**	75 (61-561)	**ρ = 0.95** **P < 0.001**	**ρ = -0.36** **P = 0.001**	**ρ = -0.29** **P = 0.011**
***L. africana* - females**	143 (67-536)	**ρ = 0.77** **P < 0.001**	**ρ = -0.17** **P = 0.040**	**ρ = 0.25** **P = 0.003**
***L. africana* - males**	37 (61-334)	**ρ = 0.98** **P < 0.001**	ρ = 0.03 P = 0.883	ρ = 0.09 P = 0.593
Elephants older than 360 months	70 (363-763)	ρ = 0.03 P = 0.820	ρ = -0.17 P = 0.149	ρ = 0.15 P = 0.205
***E. maximus* - females**	32 (377-763)	ρ = 0.10 P = 0.602	ρ = 0.32 P = 0.077	ρ = 0.28 P = 0.119
***E. maximus* - males**	10 (380-561)	ρ = 0.27 P = 0.446	ρ = -0.10 P = 0.780	**ρ = 0.86** **P = 0.001**
***L. africana* - females**	28 (363-536)	**ρ = -0.43** **P = 0.023**	**ρ = -0.66** **P < 0.001**	**ρ = 0.61** **P = 0.001**
***L. africana* - males**	-	-	-	-
Elephants older than 480 months	27 (486-763)	ρ = 0.109 P = 0.587	ρ = 0.18 P = 0.361	ρ = 0.13 P = 0.536
***E. maximus* - females**	15 (486-763)	ρ = -0.13 P = 0.643	ρ = 0.48 P = 0.068	ρ = 0.08 P = 0.774
***E. maximus* - males**	7 (542-561)	**ρ = -1.00** **P < 0.001**	**ρ = -0.95** **P = 0.001**	**ρ = 0.95** **P = 0.001**
***L. africana* - females**	5 (522-536)	ρ = -0.30 P = 0.624	ρ = -0.15 P = 0.805	ρ = 0.46 P = 0.434
***L. africana* - males**	-	-	-	-

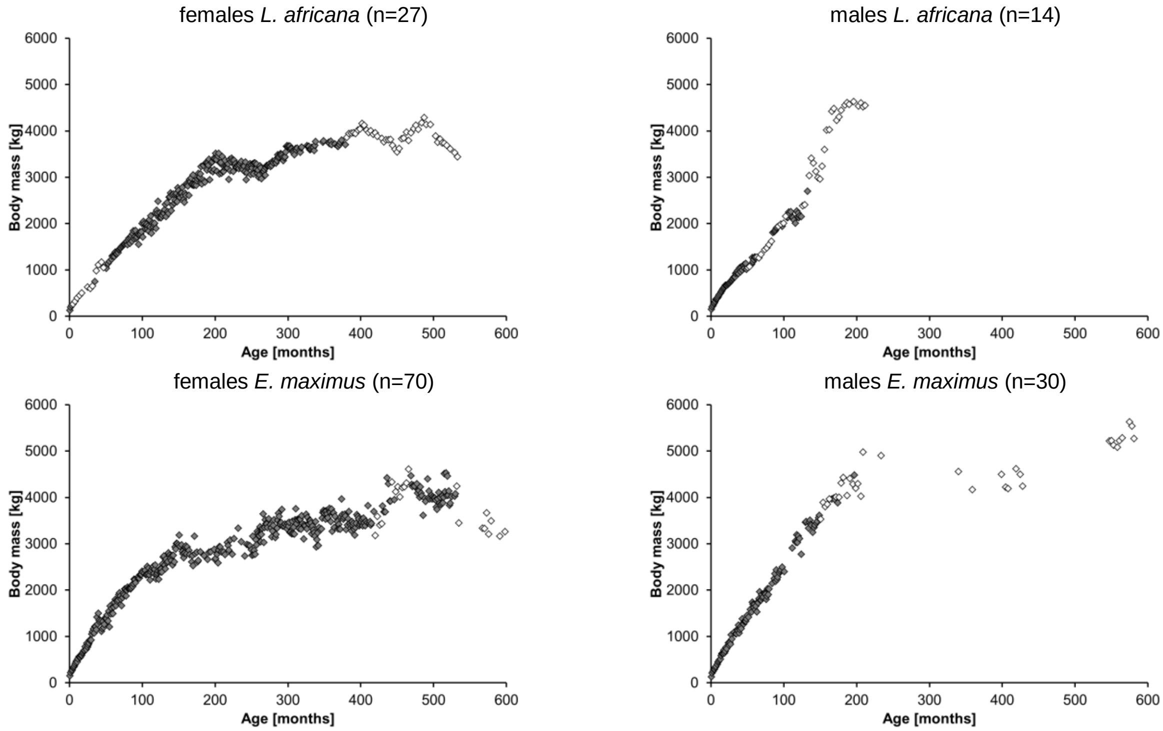

Figure 1 Temporal mean body mass development in European zoo elephants plotted separately for species and sex. Black diamonds indicate mean body mass of at least three individuals per month and open diamonds the mean of at least three body mass records per three months of one or various individuals.

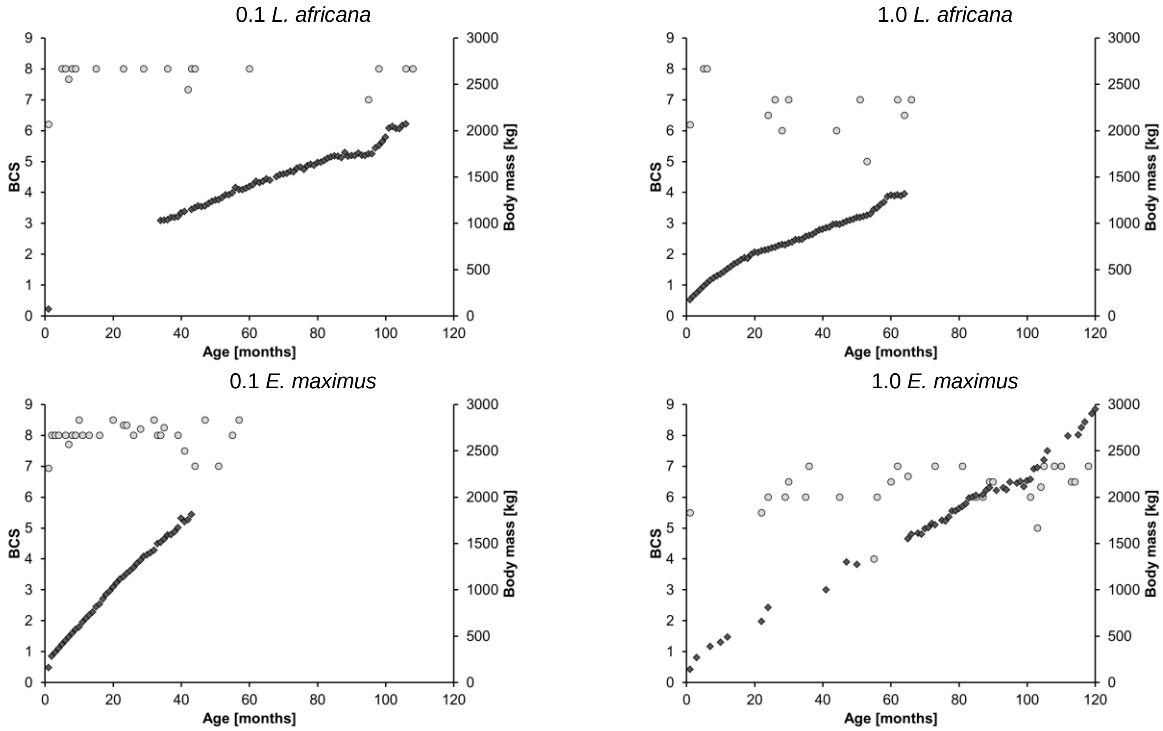

Figure 2 Temporal development of body mass (black diamonds) and body condition score (open circles) in zoo elephants under the age of 8 years

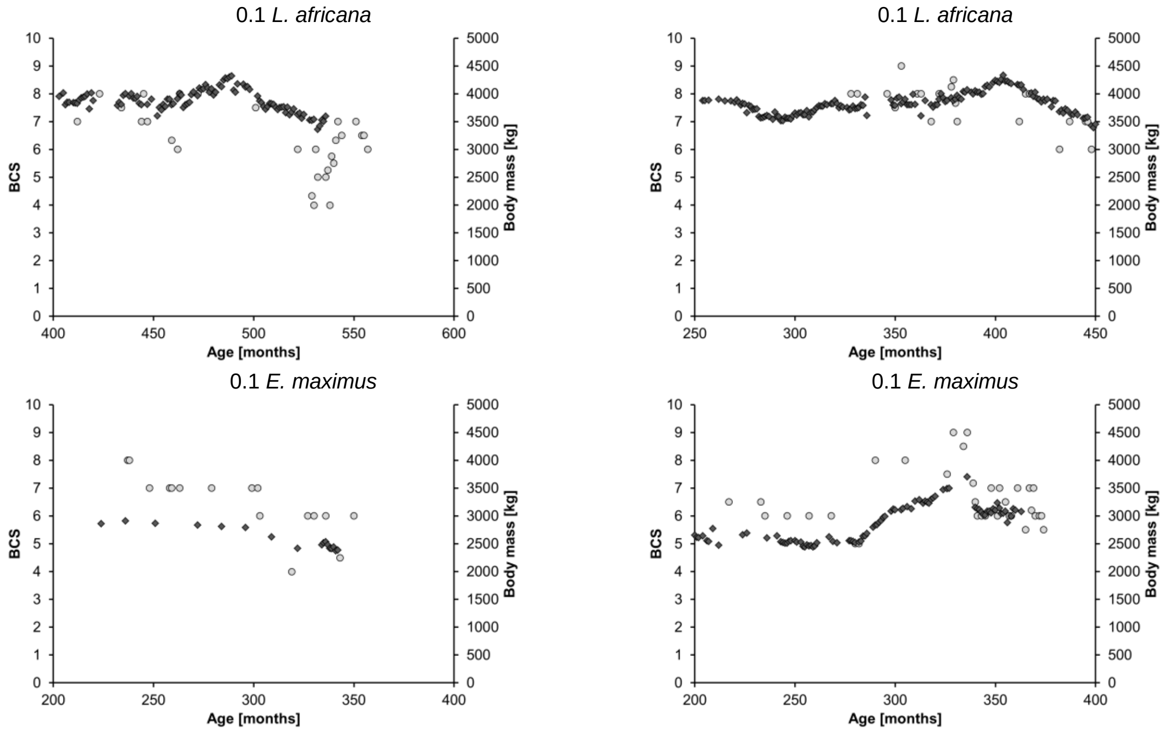

Figure 3 Temporal development of body mass (black diamonds) and body condition score (open circles) in zoo elephants over the age of 20 years

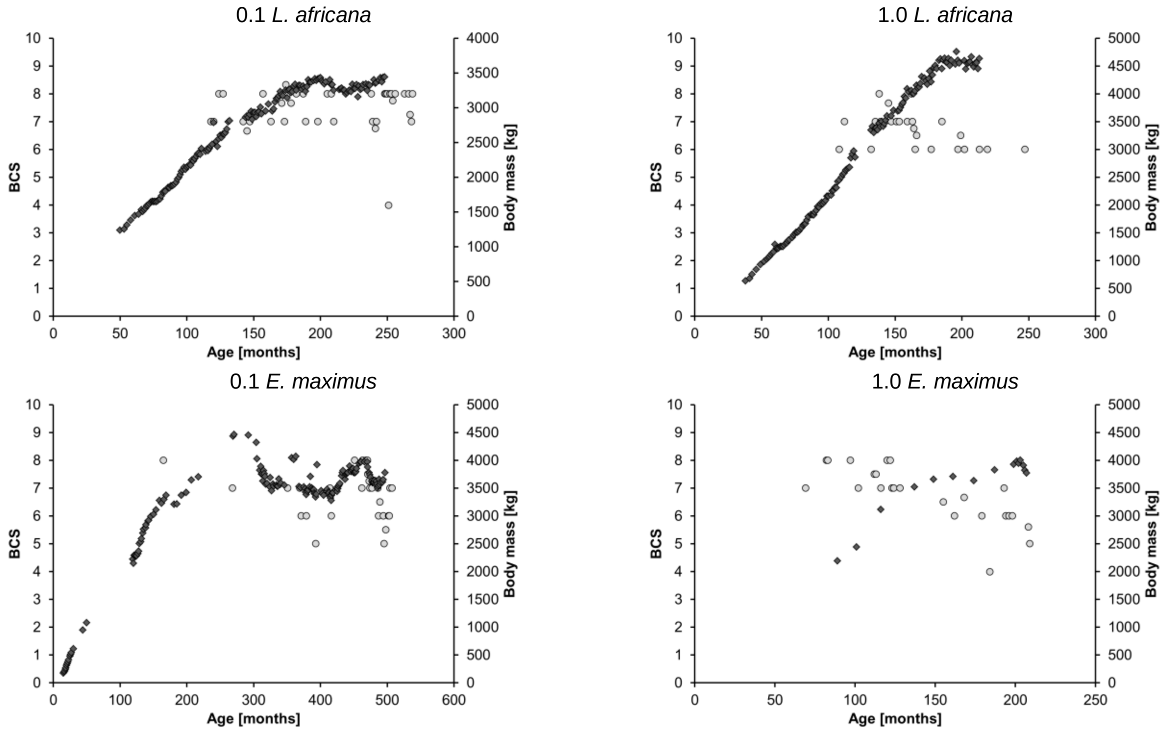

Figure 4 Temporal development of body mass (black diamonds) and body condition score (open circles) in zoo elephants between 8 and 20 years of age

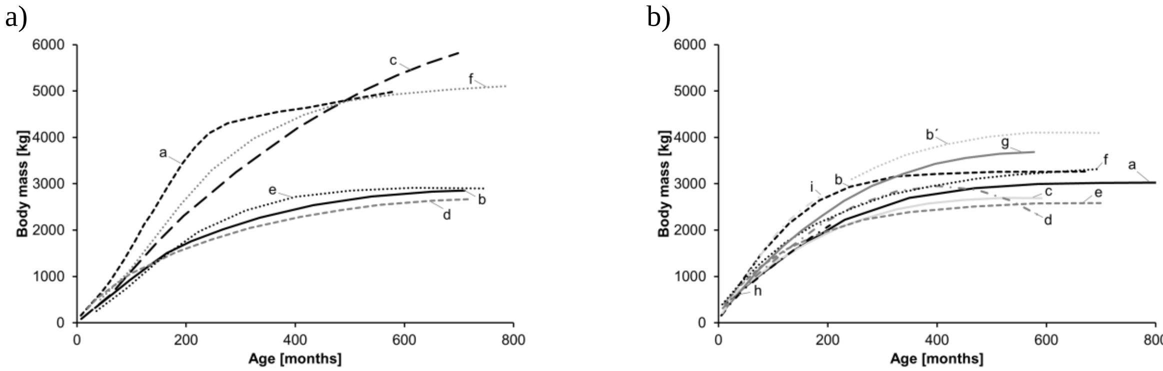

Figure 5 a) Body mass growth curves for *L. africana* reported for free-ranging males by Johnson and Buss (1965) (*a*), females (*b*) and males (*c*) by Laws (1966) and females by Hanks (1969) (*d*). Sikes (1971) reported curves for free-ranging and captive females (*e*) respectively males (*f*) in their countries of origin. **b)** Body mass growth curves reported for (semi-)captive populations of *E. maximus* in countries of origin. (*a*) females and (*b*) males in Indian Timber camps (Sukumar et al. 1988), (*c*) females and (*d*) males in Timber camps of Myanmar and Thailand (Kurt and Kumarasinghe 1998), (*e*) females and (*f*) males in Timber camps of Myanmar (Chapman et al. 2016), (*g*) captive males in Sri Lanka (Kurt and Kumarasinghe 1998) and (*h*) females and (*i*) males at a Sri Lankan orphanage (Weihs et al. 2001). (*b´*) presumed body mass growth curve for free-ranging male *E. maximus* drawn by eye taking by Sukumar et al. (1988).

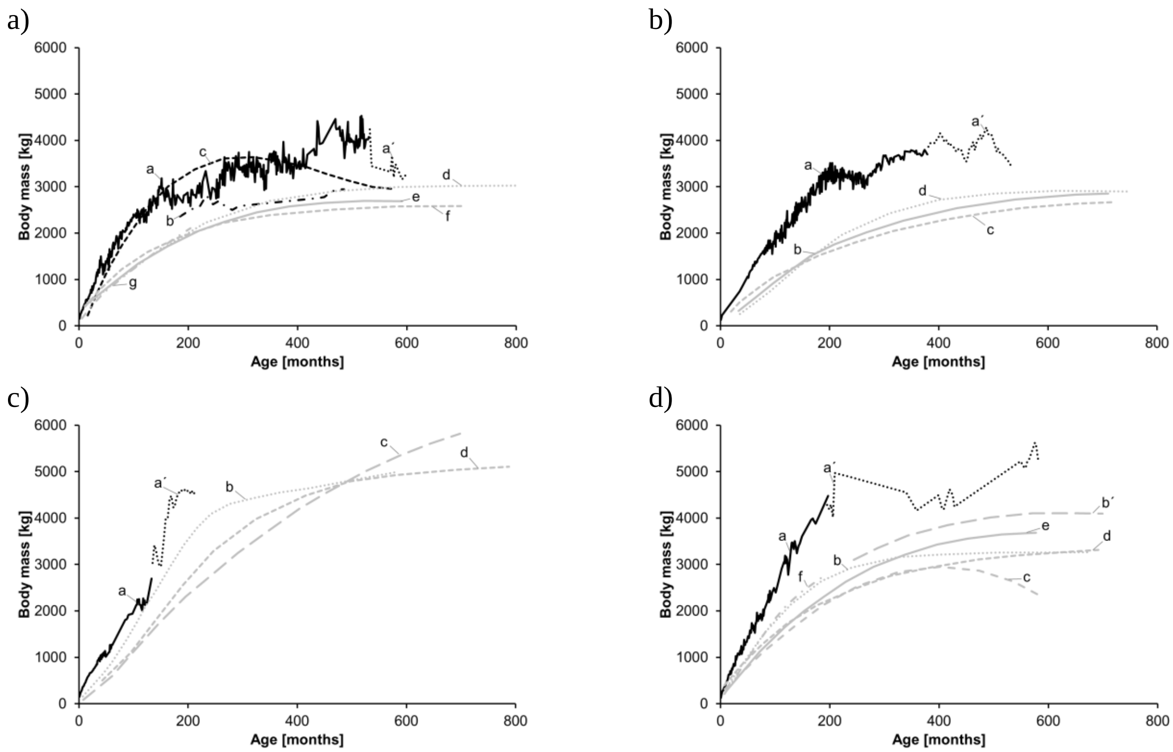

Figure 6 a) Body mass growth curves for female *E. maximus*. Our data for European zoo elephants (*a* and *a´*) and reported curves for females in (*b*) one North American zoo (Fischer et al. 1993) respectively four European facilities (*c*) by (Kurt and Kumarasinghe 1998). Literature data for semi-captive populations are given in grey (*d*: Sukumar et al. (1988), *e*: Kurt and Kumarasinghe (1998), *f*: Chapman et al. (2016), *g*: Weihs et al. (2001)). *a´* indicates data based on at least three body masses per three months as explained in the method section. **b)** Body mass growth curves for female *L. africana.* Our data for European zoo elephants (*a and a´)* in black and literature data in grey (*b*: Laws (1966), *c*: Hanks (1969), *d*: Sikes (1971)). *a´* indicates data based on at least three body masses per three months as explained in the method section. **c)** Body mass growth curves for male *L. africana.* Our data for European zoo elephants (*a and a´)* in black and literature data in grey (*b*: Johnson and Buss (1965), *c*: Laws (1966), *d*: Sikes (1971)). *a´* indicates data based on at least three body masses per three months as explained in the method section. **d)** Body mass growth curves for male *E. maximus*. Our data for European zoo elephants (*a* and *a´*) in black and literature data for (semi-)captive males in grey (*b* + *b´*: Sukumar et al. (1988), *c*: Kurt and Kumarasinghe (1998) (semi-captive), *d*: Chapman et al. (2016), *e*: Kurt and Kumarasinghe (1998) (captive) and *f*: Weihs et al. (2001)). *a´* indicates data based on at least three body masses per three months as explained in the method section. No body mass data for zoo-kept male *E. maximus* is available from the literature.

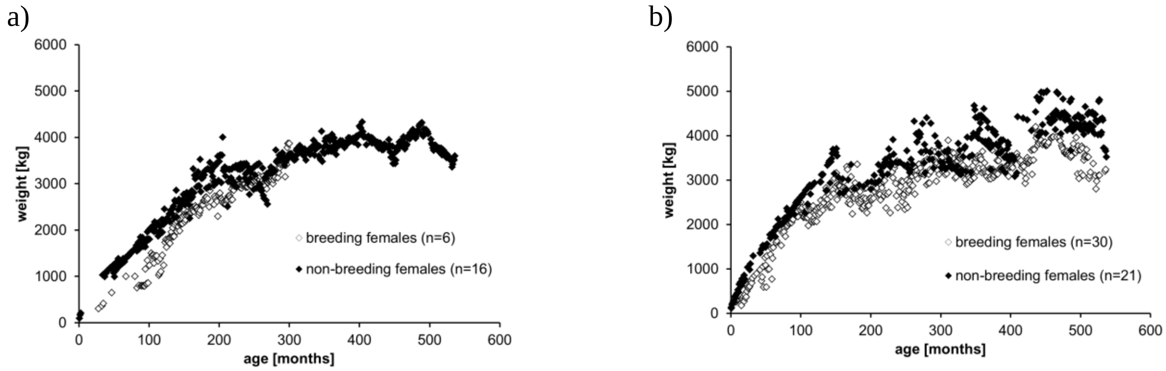

Figure 7 Development of mean body mass in breeding vs. non-breeding females of African (a) and Asian elephants (b) living in European zoos.

Elephant body mass cyclicity suggests effect of molar progression on chewing efficiency

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Under review for publication in *Mammalian Biology*

Bei der Analyse der gesammelten Gewichtsdaten Europäischer Zooelefanten konnte ein Muster in der Gewichtsentwicklung über den Lauf des Lebens festgestellt werden. Dieses war unseres Wissens bislang nicht bekannt und könnte mit der wechselnden Kauflächengröße, welche durch den horizontalen Zahnwechsel bedingt ist, zusammenhängen.

Mammalian Biology

Elephant body mass cyclicity suggests effect of molar progression on chewing efficiency

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ABSTRACT

Elephants do not replace deciduous teeth once with permanent teeth as most mammals, but replace a single cheek teeth per jaw-side five times in their lives in a process called molar progression. While this gradual process has been well-documented for the purpose of age determination, a less-considered possible side effect of this progression is that functional chewing surface fluctuates, being larger when two cheek teeth are both partially in use and smaller when only one cheek tooth is used fully. We found that body mass of both breeding and non-breeding female zoo elephants (*Elephas maximus*, *Loxodonta africana*) shows a cyclic undulation with peaks separated by many years, which is therefore unrelated to reproduction or annual seasonality. We propose variation in functional chewing surface, resulting chewing efficiency, and resulting increased food intake and/or digestive efficiency as the underlying cause. As elephants reproduce all year-round and thus are not synchronized in their molar progression pattern, climate-related fluctuations in resource availability are likely to mask this pattern in free-ranging animals. In contrast, it emerges under the comparatively constant zoo conditions, and illustrates the relevance of the dental apparatus for herbivorous mammals. The combination of variable chewing efficiency and resource availability in free-ranging elephants may render these species particularly prone to reported inter-individual fitness differences.

Keywords:

Elephant

Body mass

Growth

Molar progression

Digestion

Introduction

Reducing food particle size is crucial for herbivores, because particle size constrains the rate at which fibrous food can be digested by the symbiotic microbiota (Bjorndal et al., 1990). In mammals, teeth of various designs have evolved (Ungar, 2010) and, together with additional adaptations such as rumination, lead to variation in chewing efficiency (Fritz et al., 2009) that is linked to digestive efficiency (Clauss et al., 2015). In individual species, chewing intensity was found to compensate for variation in the availability of functional chewing surface (Pérez-Barbería and Gordon, 1998; Logan, 2003), chewing efficiency decreases with old age (Venkataraman et al., 2014), and the age-related loss of a functional dentition is usually considered an important reason for senescence and death in a variety of species (Skogland, 1988; Kojola et al., 1998; King et al., 2005), including elephants (Maglio, 1973; Lee et al., 2012). During ontogeny, the increase in the number of functional cheek teeth during adolescence (as documented in cattle, Grandl et al., 2018) or its decrease during senility (as documented in humans, Ikebe et al., 2011) are both linked to compensating changes in chewing intensity. Less functional dental chewing surface, therefore, either represents a time constraint due to the higher compensating chewing required, or a digestive constraint due to the lower chewing efficiency achieved.

In elephants, the number of functional teeth does not follow the general mammalian pattern of increase and decline from adolescence to old age. Rather than replacing a deciduous dentition with permanent teeth, elephants replace the single cheek teeth per jaw-side five times during ontogeny, with a repeated replacement of the main tooth every 10-15 years (Fig. 1, Table 1). Thus, new teeth of ever-increasing size fill the continuously growing jaw (Laws, 1966; Maglio, 1973; Roth and Shoshani, 1988; Lee et al., 2012). In this process, cheek teeth are not replaced instantaneously, but the succeeding tooth gradually enters occlusion while its predecessor is ejected piecewise by individual cranial lamellae breaking off (Laws, 1966; Roth and Shoshani, 1988). The pattern of cheek tooth replacement has been documented extensively in elephants, mainly with the aim of age determination for accurate estimates of population structure (Laws, 1966; Maglio, 1973; Roth and Shoshani, 1988; Rasmussen et al., 2005; Stansfield, 2015).

An important side effect of molar progression that has received little consideration so far is that during this process, the functional chewing surface available to the individual adult elephant fluctuates over time: it is larger when two cheek teeth are both partially in use and smaller when only one cheek tooth is used alone, with the predecessor completely ejected and the successor not yet erupted. This pattern is evident from graphical representations of ontogenetic stages in several studies that nevertheless do not mention it explicitly (Laws, 1966; Maglio, 1973; Rasmussen et al., 2005; Stansfield, 2015), was quantified (as the length of the 'grinding surface' in use during ontogenetic stages) in a study of Asian elephants (Fig. 1), and is also evident in data on the number of dental lamellae in use over time (Fig. 2). In theory, this difference could lead to compensating chewing intensity over ontogeny, with higher chewing activity at times of smaller chewing surface. However, the combination of the elephants' generally poor chewing efficiency, short digesta retention, with resulting low digestive efficiency and large portions of their daily activity budget necessarily spent in feeding (Clauss et al., 2003; Clauss et al., 2007b; Fritz et al., 2009), most likely limits the option of modulating chewing intensity. Therefore, ontogenetic differences in available chewing surface might directly translate into ontogenetic differences in chewing efficiency and hence either a reduced food intake or a lower digestive efficiency. Under a constant provision of a consistent, fibrous diet, this should result in differences in energetic gain from the diet, with resulting variation in adipose and muscle tissue reserves and overall body mass.

In the course of a study to investigate whether breeding status of zoo elephants was correlated with body condition score (Schiffmann et al., 2018), our additional aim was to test if the same trend, with nonbreeders being heavier than breeders, was also evident in body mass data. These data revealed a pattern corresponding to the considerations on molar progression above. We consider this an outstanding example of how observations made in captivity can reveal a biological peculiarity that would most likely not be recognizable in free-ranging animals.

Material and methods

As part of a study on body condition in European zoo elephants (Schiffmann et al., 2018), we collected directly measured body mass data of European zoo elephants during visits of 27 European zoological institutions. In total, 5306 data points from between 1976 and 2017 were compiled, representing 70 and 30 individual Asian elephant females and males, and 27 and 14 African elephant females and males. Body mass data were linked to the age of the respective individual at the time of weighing (in months of life). If more than one measurement per month of life was available, we calculated the mean. Subsequently, species- and sex-specific averages were calculated per month. The age range of available data exceeded the period of adolescent growth only for the females of both species. To investigate the influence of reproductive activity, we defined all females that experienced at least one live birth and rearing of a calf during their lifetime as breeders. In contrast, we categorized all females over the age of 10 years without any live births as non-breeders. All recorded data are available in the online supplement. The resulting datasets were analysed using the Gompertz equation BM=$ae^{-e(b-ct)}$, with BM body mass, *a* the asymptotic body mass and *t* the age in months. In displaying the body mass data graphically, we put it into context with the literature data on the dental eruption sequence summarized in Table 1.

Results

Body mass data linked to a specific age, with a variable number of data per individual, were available for 70 Asian (*Elephas maximus*) and 27 African (*Loxodonta africana*) elphant females. In both species, breeders did not reach the upper body masses reached by non-breeders, irrespective of whether data all individual data or data averaged for each month of age were used (Fig. 3; non-overlapping asymptotic growth parameter estimates in Gompertz models, Table 2). Visually, growth did not necessarily reach a plateau, but appeared to continue through time, dropping off in the final months of life (Fig. 3). After an initial body mass peak, body mass development over time showed a cyclicity in both breeding and non-breeding females of both species, with a duration between cycle peaks of up to 100 months (Fig. 3). In these cycles, the mean difference in body mass between peaks and nadirs was 435 kg in Asian and 288 kg in African females, respectively (Table 3).

Discussion

That being overweight may be one of the factors contributing to reproductive failure in zoo elephants has been speculated previously, based on a reported correlation of reproductive disorders and obesity in captive African females (Freeman et al., 2009; but see Chusyd et al., 2018). Our results therefore reinforce recommendations to maintain zoo elephants in a less-than-obese body condition (Hatt and Clauss, 2006; Schiffmann et al., 2018). The cyclic signal of body mass gain and loss has, to our knowledge, not been described previously. Notably, growth curves based on morphometric measurements such as shoulder height, more commonly performed in free-ranging animals (Shrader et al., 2006; Lee et al., 2013), will not reflect a cyclic reduction in body mass.

However, some similar observations exist. In a group of six captive female African elephants, a temporary body mass loss was reported for the period between 17-23 years of age; this body mass loss varied in extent between the individual elephants, but no information on the duration of this pattern is available (Walker and Schlegel, 2013). A report on free-ranging female African elephants contains some indicators of a potential body mass drop after the age of 20 years (Hanks, 1972). And it can be speculated that data from one single North American zoo (Fischer et al., 1993) support the temporary body mass drop at this age. These hints, and the fact that we observed the pattern in four different groups - the breeding and non-breeding females of each species - speak against a spurious finding.

The observed pattern must be unrelated to breeding activity, but should be associated with variation in resource provision or utilization. Given that the pattern is longer than an annual cycle, seasonally fluctuating resource provision or energy expenditures can be ruled out. We suggest that systematic ontogenetic fluctuation in chewing efficiency and hence digestive utilization of a relatively constant food supply explains the pattern. Because elephants can give birth all year round (Brown, 2014) yet often live in natural habitats with seasonal fluctuations of resource availability (Codron et al., 2012) that also lead to seasonal fluctuation in body condition (e.g. Foley et al., 2001; Pokharel et al., 2017; Ranjeewa et al., 2018), it is unlikely that a systematic cyclicity of body mass with age can be observed in free-ranging populations, because resources of differing quality are consumed by animals of all ages. The combination of variable chewing efficiency and resource availability in free-ranging elephants may render these species particularly prone to reported inter-individual fitness differences (Lee et al., 2013).

In zoos, by contrast, dietary resources are mostly kept constant, so that animals of all ages will be exposed to a much more consistent resource quality, allowing age-specific differences in resource utilization to emerge. Putative differences in feeding regimes between zoos and within zoos over time, and putative differences in adjustments of feeding and enrichment management aimed at achieving a stable body mass or preventing obesity in the various zoos, cannot be taken into account in the present study. We expect these factors to be of a lesser magnitude than the general difference in a constant and ample supply of food in captivity as compared to natural habitats, as evident in the general difference in body condition documented repeatedly between free-ranging and zoo animals (reviewed in Schiffmann et al., 2018).

Therefore, attempts at replicating and expanding our findings should focus on zoo animals - for example, body mass data of the North American and Asian zoo elephant populations -, and, relying on particular investigator perseverance, on monitoring adult elephants for their body mass by weighing, dental status by taking dental imprints (Rasmussen et al., 2005) during training sessions, and both food intake measured by weighing food offered and refused for several days (Clauss et al., 2003) and chewing efficiency measured as faecal particle size (Fritz et al., 2012) on a defined diet, over decades. When judging the body mass of their elephants, zoo managers should keep a potential fluctuation due to molar progression in mind.

Elephant molar progression has, so far, only been studied in relation to age determination (Laws, 1966; Roth and Shoshani, 1988) and not to tooth functionality. Differences in size, and possibly also in the exact timing of replacement between maxillary and mandibular molars, make it difficult to predict specific ages of optimal chewing efficiency, even when inter-individual differences are ignored. Thus, the available data on elephant tooth replacement (Table 1) is not of a quality that would allow correlating our data with ages of specific dental states. Therefore, the alternative hypothesis that it is not variation in functional chewing surface but some sensitivity caused by certain eruption processes that causes variation in food intake cannot be refuted, although the gradual process of elephant molar progression (Laws, 1966; Roth and Shoshani, 1988) may make this hypothesis seem unlikely. Although the molar eruption patterns are assumed to be similar for both species (Roth and Shoshani, 1988), the course of the body mass undulation (Fig. 3) suggests that molar eruption could occur somewhat earlier in Asian than African elephants, and that each molar has not only one but possibly several states of optimum functionality. Whether the finding that body mass fluctuations are more distinct in Asian elephants than in African elephants is spurious or has biological meaning cannot be decided. Given that available data suggests that Asian elephant have a slightly higher digestive efficiency than African elephants (reviewed in Clauss et al., 2007a), it could be speculated that a higher chewing efficiency could have a more pronounced effect in this species.

The only study that has, to our knowledge, so far investigated the functional chewing surface of proboscids across age classes, with a major focus on mammuths (Anders and von Koenigswald, 2013), provided patterns that neither clearly contradict or corroborate a pattern of a fluctuation of this measure with age. More detailed investigations on skull specimens could help further define the different stages of molar functional surface, in relation to eruption and progression and in relation to age.

Acknowledgments

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Data availability

Anonymized original body mass data will be provided as electronic supplementary material or uploaded in dryad - depending on the decision of the editor.

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Table 1. Compilation of literature data on molar replacement in elephants

Species	Living conditions	Eruption M1	Replacement (=loss) M1	Eruption M2	Replacement (=loss) M2	Eruption M3	Replacement (=loss) M3	Eruption M4	Replacement (=loss) M4	Eruption M5	Replacement (=loss) M5	Eruption M6	Reference
		---------- [years of life] ----------											
not indicated	not indicated	0.25		3		5		10		20		30	1
L. africana	free-ranging		2-2.5	1.5	5	2	9	5	17	10	45	20	2
L. africana	free-ranging		2		6		13-15		28		43	30	3
L. africana	free-ranging	0	2	1.5	5	2	11	5	19	15	60	23	4
L. africana	not indicated		2		4-5								5
L. africana	captive zoo		2-3		5		10-11		24-25		35		6
L. africana	not indicated		2		6		15		28		47		7
L. africana	not indicated		2-3		4-6		9-12		18-28		40-50		8
E. maximus	not indicated		2		5		9						9
E. maximus	free-ranging							9	25	25	55		10
E. maximus	not indicated		2-3		4-6		9-12		18-28		40-50		11
E. maximus	not indicated	0.33	2-2.5	0.5	6	3	9	6	25	20	50-60	40	12
mean *L. africana*		0.06	2.06	1.17	5.13	2.10	11.71	5.00	23.36	13.00	45.14	26.50	
mean *E. maximus*		0.33	2.25	0.50	5.33	3.00	9.50	7.50	24.33	22.50	51.67	40	
mean both species		0.18	2.11	1.40	5.18	2.86	11.05	6.67	23.65	17.33	47.10	30.75	
mean both species in months of life		2.12	25.36	16.80	62.18	34.32	132.60	80.00	283.80	208.00	565.20	369.00	

References: 1 (Frade, 1955), 2 (Johnson and Buss, 1965), 3 (Laws, 1966), 4 (Krumrey and Buss, 1968b), 5 (Sikes, 1971), 6 (Lang, 1980, 1994), 7 (Keet, 1991; cited in Jarofke, 2007), 8 (Shoshani, 1992), 9 (Cornwall, 1956), 10 (Momin Khan, 1977), 11 (Shoshani, 1992), 12 (Kalita and Sarma, 2003; cited in Fowler and Mikota, 2006)

Table 2 Gompertz growth models comparing growth parameters of breeding (Br) and non-breeding (Non-Br) female elephants. Models (BM=$ae^{-e(b-ct)}$) were fitted to either averages across all individuals per time point (month, *t*). Note the differences in asymptotic body mass (*a*).

Species	**Group**	***n***	***a* (95% CI) asymptotic body mass**	***b* (95% CI)**	***c* (95% CI)**
			Average monthly body mass		
Elephas	Br	485	3416 (3372 to 3460)	0.63 (0.56;0.71)	0.013 (0.012;0.014)
maximus	Non-Br	453	3959 (3903 to 4016)	0.61 (0.52;0.71)	0.012 (0.011;0.013)
Loxodonta	Br	246	3620 (3541 to 3699)	1.42 (1.30;1.54)	0.014 (0.013;0.015)
africana	Non-Br	475	3888 (3860 to 3916)	0.95 (0.89;1.01)	0.014 (0.013;0.015)
			Individual data		
Elephas	Br	1199	3382 (3342 to 3423)	0.67 (0.59;0.74)	0.014 (0.013;0.015)
maximus	Non-Br	758	3984 (3934 to 4033)	0.64 (0.55;0.72)	0.012 (0.011;0.013)
Loxodonta	Br	568	3594 (3498 to 3690)	1.35 (1.21;1.48)	0.013 (0.012;0.014)
africana	Non-Br	1328	3901 (3864 to 3938)	0.97 (0.92;1.03)	0.014 (0.013;0.014)

Table 3 Change in body mass (BM, kg) between successive peaks and nadirs in breeding (Br) and non-breeding (Non-Br) adult female elephants for the period after asymptotic growth was reached (i.e. after 200 months in age).

	Br				Non-Br			
Phase	**Start**	**End**	**BM mean**	**ΔBM**	**Start**	**End**	**BM mean**	**ΔBM**
Elephas maximus								
Nadir 1	200	240	3300		220	260	2832	
Peak 1	250	290	3655	355	280	320	3368	536
Nadir 2	310	350	3580	75	350	390	3294	74
Peak 2	350	390	3937	356	430	470	3807	513
Nadir 3	390	430	3627	309	500	540	3402	405
Peak 3	460	500	4364	737				
Nadir 4	570	610	3371	993				
Loxodonta africana								
Nadir 1					200	240	2880	
Peak 1	200	240	3594		290	330	3515	635
Nadir 2	290	330	3619	25				
Peak 2	380	420	3983	365				
Nadir 3	430	470	3768	215				
Peak 3	480	520	3944	176				
Nadir 4	510	550	3629	315				

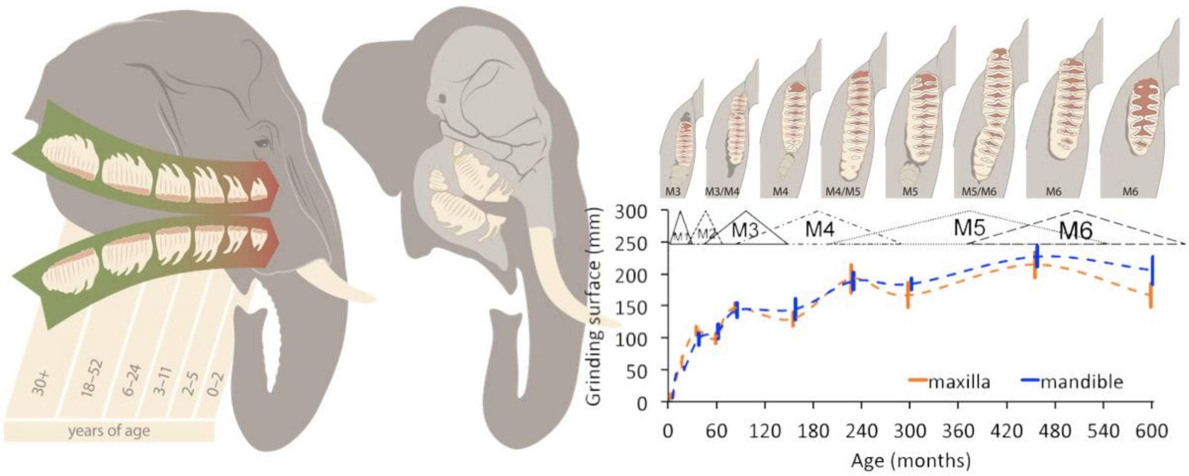

Figure 1 Visualisation of the sequence of tooth replacement in elephants with age, indicating the progression of the six molars in an African elephant, the placement of teeth at a certain moment of the progression sequence in the jaw bones in an Asian elephant, the variation in the length of the molar 'grinding surface' at estimated age points and the extrapolated undulating time course in Asian elephants based on literature data (Roth and Shoshani, 1988) compared to molar replacement periods (modified from Johnson and Buss, 1965) according to literature (Table 1), with pictograms of the mandibular molar surface of African elephants adapted from published drawings (Laws, 1966). M1-M6: molar 1-6. Triangles indicate the duration of a molars' presence from eruption to its loss. Pictograms not to scale. *©2018 Vetcom – Pascal Glatzfelder*

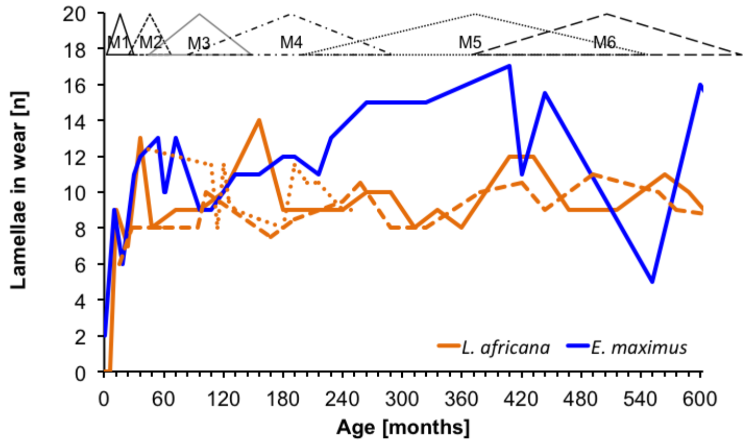

Figure 2 Number of molar lamellae simultaneously in use in relation to age in African elephants (*Loxodonta africana*) (full line Laws, 1966; dots Krumrey and Buss, 1968a; interrupted line Lee et al., 2012) and Asian elephants (*Elephas maximus*) (Roth and Shoshani, 1988) compared to molar replacement (modified from Johnson and Buss, 1965) according to literature (see Table 1). Note that all lamellae in wear irrespective of their size were counted. Also, age determination was derived from dental configuration in most of these studies (except Lee et al., 2012), leading to somewhat circular reasoning. The main message of this figure is that there is inter-individual (or inter-study) variability, and variation in the morphology of the occlusal molar surface over time. M1-M6: molar 1-6. Triangles indicate the duration of a molars' presence from eruption to its loss.

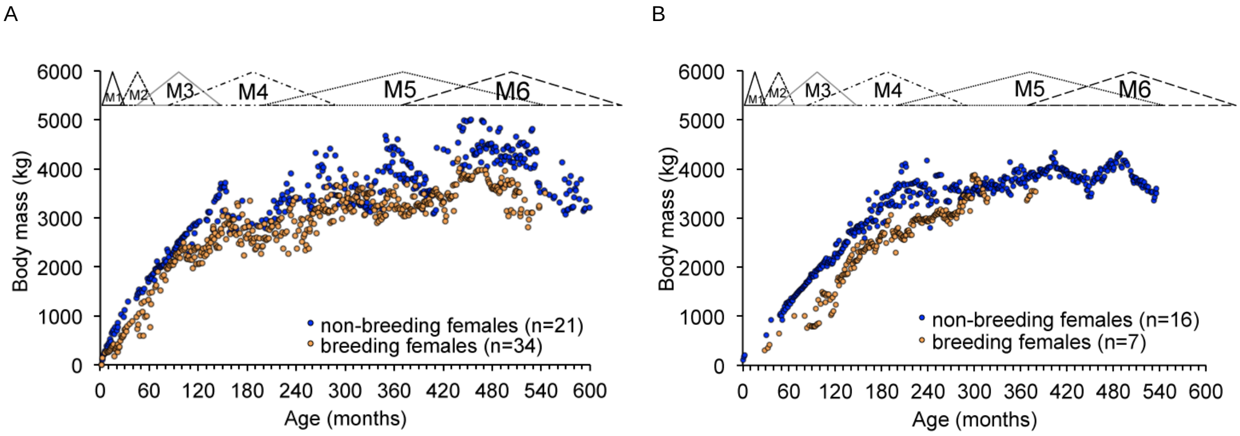

Figure 3 Mean monthly body mass development in breeding vs. non-breeding females of **(A)** Asian and **(B)** African zoo elephants compared to molar replacement (modified from Johnson and Buss, 1965) according to literature (see Table 1). M1-M6: molar 1-6. Triangles indicate the duration of a molars' presence from eruption to its loss.

Online archive www.elephants-of-europe.org

Published on 16.06.2018

Um den Elefantenhaltern Europas die gesammelten BCS-Daten verfügbar und im Sinne eines Monitoring-Tools langfristig nutzbar zu machen, wurde das Online-Archiv **„www.elephants-of-europe.org“** entwickelt. Am 16.06.2018 wurde das Archiv den Verantwortlichen der Haltungsstätten zugänglich gemacht.
Das Archiv wird von mir kontinuierlich gepflegt: Zusendungen von Zoos oder Privatpersonen (90 seit dem 16.06.2018) sowie von mir selbst aufgenommene Fotografien (122 seit dem 16.06.2018) werden einheitlich beurteilt, und die Fotos zusammen mit dem resultierenden Body Condition Score den entsprechenden Zoos zugänglich gemacht.

When elephants fall asleep: a literature review on elephant rest with case studies on elephant falling bouts, and practical solutions for zoo elephants

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RESEARCH REVIEW WITH CASE STUDIES

WILEY ZOOBIOLOGY

When elephants fall asleep: A literature review on elephant rest with case studies on elephant falling bouts, and practical solutions for zoo elephants

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Little attention has been paid to the resting and sleeping behavior of zoo elephants so far. An important concern is when elephants avoid lying down, due to degenerative joint and foot disease, social structure, or stressful environmental changes. Inability or unwillingness to lie down for resting is an important welfare issue, as it may impair sleep. We emphasize the importance of satisfying rest in elephants by reviewing the literature on resting behavior in elephants (*Loxodonta africana* and *Elephas maximus*) as well as the documentation of four cases from European zoos and our own direct observations in a zoo group of four female African elephants during 12 entire days. The common denominator in the case reports is the occurrence of a falling bout out of a standing position subsequently to a cessation of lying rest for different periods of time. Although well-known in horses as "episodic collapse" or "excessive drowsiness," this syndrome has not been described in elephants before. To enable its detection, we recommend nocturnal video monitoring for elephant-keeping institutions. The literature evaluation as well as own observational data suggest an inverse relationship between lying rest and standing rest. Preventative measures consist of enclosure modifications that facilitate lying rest (e.g., sand hills) or standing rest in a leaning position as a substitute. Anecdotal observations suggest that the provision of appropriate horizontal environmental structures may encourage safe, sleep-conducive standing rest. We provide drawings on how to install such structures. Effects of providing such structures should be evaluated in the future.

KEYWORDS
elephant, leaning, lying rest, sleep, zoo

1 | INTRODUCTION

Modern zoos have achieved many improvements in elephant husbandry and management during the past years (Greco, Meehan, Hogan et al., 2016; Greco, Meehan, Miller et al., 2016). In doing so, studies on natural behavior of elephants supplied basic information concerning their needs. Most probably due to challenging observation conditions, only little research on nocturnal behavior of free-ranging elephants has been conducted yet, leaving few "natural benchmark" data in particular with respect to sleeping behavior.

Evans (1910) already postulated that "it is of outmost importance that the elephant should have his sleep…" and common sense alone might suggest satisfying resting behavior to be of even higher priority in stressed, physically ailed, or geriatric elephants. Experimental studies in rats confirmed negative health impact of sleep deprivation, leading to death unless the deprivation was reversed (Rechtschaffen & Bergmann, 2002). For elephants, sleep might be linked to the opportunity to lie down. Gonfalone and Jha (2015) suggest that rapid eye movement (REM) sleep, a state characterized by general loss of voluntary muscle tone, is only possible when the animal does not have to actively support its body against gravity. This correlation might explain the small amount of REM sleep in birds as well as cetaceans and otarids on days out at sea (Gonfalone & Jha, 2015; Siegel, 1995). In the latter, this feature might not mainly be due to gravity but represent a mechanism to avoid drowning. Assuming that elephants need a certain but unknown amount of REM sleep, this would mean that due to gravity, this is only possible when they lie down or lean, allowing sufficient relaxation of musculature. In contrast, a free-standing position requires constant tension of anti-gravity musculature. Although no scientific evidence exists, it seems reasonable to assume that free-standing elephants might only achieve slow wave sleep, and not enter REM sleep unless they are lying down or leaning. In horses, Williams et al. (2008) demonstrated the occurrence of REM sleep during lying rest, while a stable standing position could not be sustained when entering the state of REM sleep.

Moreover, several case reports demonstrated "episodic collapse" or a state called "excessive drowsiness" in horses, subsequent to prolonged deprivation of recumbent sleep (Bertone, 2006; Coomer & Fouché, 2010; Lyle & Keen, 2010). Bertone (2006) reported cases of two domestic horses that became reluctant to lie down, one due to abdominal pain with discomfort in lying position, and the other due to relocation to a new facility. This investigator postulated three categories of causes for avoidance of lying rest in horses. These are 1) pain-associated; 2) environmental insecurity-associated; and 3) monotony-induced. More than one category might occur at the same time (Coomer & Fouché, 2010). Affected horses have been shown to regenerate uneventfully once a satisfying amount of sleep is regained (Bertone, 2006). Horses are supposed to require 30–60 min of REM sleep in recumbent position per 24 hr (Coomer & Fouché, 2010).

Pathological fatigue should be differentiated from cataplexy and muscular atonia occurring in narcolepsy, caused by a pathologic alteration in the central nervous system (Bertone, 2006; Mignot & Dement, 1993). In contrast to "episodic collapse" due to "excessive drowsiness," narcolepsy occurs while animals are fully engaged in a task or meet an exciting situation. Thus, episodes of narcolepsy can be elicited repeatedly by presentation of the corresponding circumstances. In contrast, "episodic collapse" or "excessive drowsiness" occur in moments of increased relaxation (Bertone, 2006). To our knowledge, neither episodic collapse/excessive drowsiness nor narcolepsy have ever been reported in elephants so far. However, observations of three individual elephants that showed a falling bout after a period of lying rest deprivation suggested that excessive drowsiness might occur in elephants, too (Box 1).

BOX 1. Individual collapse bouts in three zoo-kept elephants

A – male African elephant, 18 years old

The male had lying rest exclusively on the left probably due to a chronic pulpitis on his right tusk. Staff found him in a recumbent position on the 22nd of January 2014. Video footage showed standing rest with slightly leaning against a wall before his hindquarters gave way and he fell on his right side. The elephant was turned on his left side at 12.14 pm, from where he got up. No substantial hematological and biochemistry changes were detectable. The elephant recovered from his fall and no further incident occurred. At present, he is mostly lying on his right side making use of sand piles.

B – female Asian elephant, 27 years old

Checking pre-partum video records revealed an incident of falling on her left side out of standing position on the 14th of March 2012. Having standing rest, her hindquarters gave way and she hit the sand floor with her left side. After falling, she seemed to struggle for orientation before getting back on her feet. The incident lasted less than 1 min. The cow gave birth on the 9th of April 2012. No further incident of falling occurred.

Falling sequence of the female Asian elephant (*Elephas maximus*) (©Zoo Leipzig)

C – female Asian elephant, 60 years old

This elephant suffered from chronic degenerative joint disease and ceased to lay down in 2014. Staff found her in a recumbent position on the October 14th, 2015. Video recordings revealed her to have standing rest before her hindquarters gave in and she fell on her right side. Staff succeeded in bringing her back on her feet within hours. No significant alterations in blood values occurred. The female recovered well from the incident and started having rest exclusively in locations allowing her to lean on, whereas she preferred a free-standing position before her fall.

for more detailed case descriptions, see online supplementary S1

In stressed, ill, or geriatric elephants, a general shift from lying to standing rest has been reported (Holdgate et al., 2016; Laws et al., 2007; Walsh, 2017; Wuestenhagen, Weisz, & Schwammer, 2000), which is typically interpreted as the result of the animal's anticipation that it may have difficulties getting up again. A variety of causes may make an elephant reluctant to lie down (Table 1). Although variable in nature, all these factors result in a lack of restorative sleeping behavior of an individual elephant. It should be noted that depending on their occurrence, such factors might be considered more or less serious. As an example, reluctance to lie down due to guarding of a new-born calf will occur only temporarily, while lying sleep avoidance caused by an inappropriate substrate might persist over years. Deprivation due to not feeling sufficiently secure has also been reported in elephants and might occur temporarily or constantly, depending on the underlying cause (Table 1). In rats as well as in cats, failure to enter REM sleep due to insufficient relaxation caused by an insecure position (on a very small platform over a water body) has been documented (Gonfalone & Jha, 2015; Rechtschaffen & Bergmann, 2002). With respect to these findings, it appears well possible that elephants are reluctant to adopt a lying position, which would allow REM sleep, when they feel vulnerable, unsafe, or unable to get up again.

With this contribution, we want to draw attention to the problem of sleep deprivation caused by the avoidance of lying rest in zoo elephants. We suggest a potential, practical leaning opportunity in standing rest for affected elephants.

2 | REVIEW METHOD AND STATISTICAL ANALYSIS

We conducted a literature research using common online search engines (pubmed and google scholar) using combinations of search the terms “elephant,” “sleep,” “rest,” “activity budget,” “standing,” and “leaning,” as well as monographs by recognized experts in elephant behavior and ecology (Douglas-Hamilton, 1972; Kurt, 1986; Moss, Croze, & Lee, 2011; Sukumar, 1989). We collected literature thus identified with the help of the library services of the Vetsuisse Faculty, University of Zurich, including their e-journal collection. From this literature, we extracted data available on the basis of individual animals for age, the time spent in lying and in standing rest, and the laterality of lying rest, and compiled them per elephant species in a spreadsheet, which is available as online supplementary S2. Several current publications on nocturnal elephant behavior lack data on individual

TABLE 1 Factors reported to correlate with reluctance to lie down in zoo elephants

Causing factor	Explanation	Reference
Physical environment		
Solid ground	Hard substrate makes lying down uncomfortable for elephants.	Roocroft (2005)
Recent arrival at new facility	Elephant does not feel sufficiently safe to lie down in its unfamiliar environment.	Laws et al. (2007)
Environmental novel stressors	Elephant does not feel comfortable enough to lie down.	Kandler (2010); Koyama et al. (2012)
Social environment		
Presence of human observers	Elephants are suspicious and lie down for short periods only.	Hartmann, Bernstein, and Wilson (1968)
Recent arrival at new facility	Elephant does not feel sufficiently safe to lie down in its unfamiliar environment.	Laws et al. (2007)
Social novel stressors	Elephant does not feel comfortable enough to lie down.	Koyama et al. (2012)
Social conflict and subdominant social rank	Elephants experience a certain tension by the presence of a conspecific and are not sufficiently relaxed to lie down.	Kandler (2010); Walsh (2017)
Dominant social rank	Due to its leadership, a dominant elephant may guard sleeping herd mates in standing position.	Kandler (2010)
Physical state of an elephant		
Severe arthrosis	Front limbs with poor range of motion complicate getting down and up again.	Kandler (2010); Roocroft (2005); Wuestenhagen et al. (2000)
Poor musculature and strength	Elephant fears being unable to get up again and thus avoids lying down.	Braidwood (2013)
Reproductive activities	Male does not lie down to sleep when female group with one female in estrus is housed with him overnight.	Walsh (2017)
Maternal care post-partum	Elephant females express shorter bouts of lying rest and stay in upright position guarding their new-born calves.	Walsh (2017)
Personality of an elephant		
Vigilant personality	Elephant does not feel sufficiently safe to lie down.	Williams et al. (2015)

TABLE 2 Literature overview on quantitative studies on elephant resting and sleeping behavior

Species; conditions	Method of observation and duration (hours)	Averaged daily duration of lying rest (hours)	Averaged daily duration of standing rest (hours)	Averaged total daily duration of rest (hours)	Lying and standing sleep recorded	Phase of major sleep	Leaning observed	Reference
E. max.; cc	Direct; 12	4.61	Not recorded	4.61	No, only lying	Not reported	No	Gebbing (1959)
E. max.; cz	Direct; 12	3.67	Not recorded	3.67	No, only lying	Not reported	No	Gebbing (1959)
E. max.; cc	Direct; 8	4.57	0.35	4.92	Yes	11.00pm–07.00am	No	Kurt (1960)
E. max.; crc	Direct; 24	Not specified	Not specified	3.71	Yes	Not reported	No	Kurt (1986)
E. max.; cc	Camera recordings; 11	3.29	0.23	3.52	Yes	01.00am–04.00am	Yes, against wall or fence	Tobler (1992)
E. max.; cz	Camera recordings; 17	4.13	2.18	6.31	Yes	01.00am–04.00am	Yes, against wall or fence	Tobler (1992)
E. max.; cc	Camera recordings; 24	3.60	Not recorded	3.60	No, only lying	00.00am–04.00am	No	Friend (1999); Friend and Parker (1999)
E. max.; co	Direct; 8	3.56	0.51	4.07	Yes	00.00am–06.00am	No	Kurt et al. (2001)
E. max.; cz	Camera recordings; 15	1.96	5.06	7.02	Yes	Not reported	No	Meller et al. (2007)
E. max.; cz	Camera recordings; 15	3.71	Not recorded	3.71	No, only lying	Not reported	No	Björk (2011)
E. max.; cz	Camera recordings; 12	3.23	Not recorded	3.23	No, only lying	11.00pm–06.00am	No	Ibler and Pankow (2012)
E. max.; cz	Camerea recordings; 16.5	2.43	3.01	5.44	Yes	10.00pm–06.00am	No	Williams et al. (2015)
E. max.; cz	Accelerometers in anklets; 24	3.6	Not recorded	3.6	No, only lying	01.00am–05.00am	No	Holdgate et al. (2016)
E. max.; cz	Camera recordings; 13	4.27	Not recorded	4.27	No, only lying	Not reported	No	Walsh (2017)
E. max.; co	Camera recordings; 11.5	Not specified	Not specified	Not specified	Yes	11.00pm–01.00am and 03.30am–05.30am		Stokes et al. (2017)
L. afr.; f	Direct; 24	Not specified	Not specified	1.12	Yes	Small hours of the morning	No	Wyatt and Eltringham (1974)
L. afr.; cz	Direct; 11	4.17	Not recorded	4.17	No, only lying	9.00pm–11.00pm and 03.00am–05.00am	No	Khueme (1963)
L. afr.; cz	Camera recordings; 13	2.63	Not recorded	2.63	No, only lying	02.00am–05.00am	Yes, against wall	Weisz et al. (2000); Wuestenhagen et al. (2000)
L. afr.; cz	Camera recordings; 16	3.16	2.32	5.48	Yes	01.00am–06.00am	No	Kandler (2010)
L. afr.; cz	Direct and camera recordings; 24	2.80	Not recorded	2.80	No, only lying	Not reported	No	Posta et al. (2013)

(Continues)

TABLE 2 (Continued)

Species; conditions	Method of observation and duration (hours)	Averaged daily duration of lying rest (hours)	Averaged daily duration of standing rest (hours)	Averaged total daily duration of rest (hours)	Lying and standing sleep recorded	Phase of major sleep	Leaning observed	Reference
L. afr.; cz	Direct and camera recordings; 24	Not specified	Not specified	2.20	Not specified	11.00pm–05.00am	No	Horback et al. (2014)
L. afr.; cz	Camera recordings; 10	Not specified	Not specified	7.86	Yes	Not reported	No	Rönnborn (2014)
L. afr.; cz	Direct and camera recordings; 21.5	4.60	6.97	11.57	Yes	11.00pm–05.00am	No	Boyle et al. (2015)
L. afr.; cz	Accelerometers in anklets; 24	2.1	Not recorded	2.1	No, only lying	01.00am–05.00am	No	Holdgate et al. (2016)
L. afr.; *f*	Actiwatches; 24	0.28	1.77	2.05	Yes	01.00am–06.00am	No	Gravett et al. (2017)
L. afr.; cz	Direct; 24	1.01	3.86	4.87	Yes	00.00am–06.00am	Yes	This study

f, free-ranging; cc, captive circus, co, captive orphanage; cz, captive zoo; crc, captive recently captured.

elephants, sleeping activity and could not be considered in our analysis (Holdgate et al., 2016; Horback, Miller, Andrews, & Kuczaj, 2014; Stokes, Perera, Jayasena, & Silva-Fletcher, 2017). We performed correlation analysis by nonparametric Spearmans' test, and General Linear Models (GLM; confirming the normal distribution of residuals by Kolmogorov-Smirnov-test) for Asian elephants to include both the effect of origin (zoo, circus, or orphanage) and age in the analyses. Due to a lack of corresponding data, we could not investigate origin in African elephants. All analyses were performed in SPSS 23.0 (IBM, Armonk, NY) with the significance level set to 0.05.

3 | RESULTS

Table 2 gives an overview on the literature of quantitative studies on elephant resting and sleeping behavior under free-ranging and different captive conditions. For the African species, daily lying rest durations have been identified in two adult females, while such quantitative results from the wild are lacking for the Asian species (Gravett et al., 2017). In the wild, African elephants have been observed to go for up to 9 days without lying down to sleep (Paul

TABLE 3 Nonparametric correlations in zoo elephants of age (years) with the hours per day spent lying, standing, total resting, and the percentage of lying spent in left recumbency

	Lying hours	Standing hours	Total hours	Percent left
African elephants (*Loxodonta africana*)				
Age	**R = −0.79 p < 0.001 n = 33**	**R = 0.88 p = <0.001 n = 19**	R = 0.15 p = 0.481 n = 25	R = 0.05 p = 0.935 n = 5
Lying hours		**R = −0.715 p = 0.001 n = 19**	R = 0.14 p = 0.565 n = 20	R = 0.00 p = 1.000 n = 5
Standing hours			**R = 0.48 p = 0.039 n = 19**	n.a.
Total hours				n.a.
Asian elephants (*Elephas maximus*)				
Age	**R = −0.50 p < 0.001 n = 59**	**R = 0.42 p = 0.020 n = 31**	**R = −0.36 p = 0.038 n = 34**	R = 0.224 p = 0.462 n = 13
Lying hours		**R = −0.636 p < 0.001 n = 31**	**R = 0.40 p = 0.019 n = 34**	R = −0.29 p = 0.334 n = 13
Standing hours			R = 0.25 p = 0.167 n = 31	R = 0.08 p = 0.829 n = 10
Total hours				R = −0.121 p = 0.694 n = 13

n.a., not analyzed for lack of sufficient data points. Data from Figure 1. Bold values signify p < 0.05.

Manger, personal communication). Researchers found Asian elephants to express phases of lying rest in the wild, and expect them to be short considering how rarely they are observed (Kurt, 1986; McKay, 1973). Closest to the situation in the wild might be the observations by Kurt (1986), who measured resting time of recently captured elephants in a Khedda, although high stress levels under these circumstances might have significantly influenced these findings.

Only a few studies investigating activity budgets of zoo elephants included complete 24 hr observation, namely Posta et al. (2013), Horback et al. (2014), Holdgate et al. (2016), and the present study (Table 2). The duration of lying rest and standing rest in zoo elephants varied considerably across different studies (see Table 2). A comprehensive survey on zoo elephants in the UK revealed that 64.6% often laid down, while 6.4% never did so (Harris, Sherwin, & Harris, 2008). These values differed from a sample of extensively kept Asian elephants in India, out of which 97.6% laid down often and only 2.4% did not lay down at all (Harris et al., 2008).

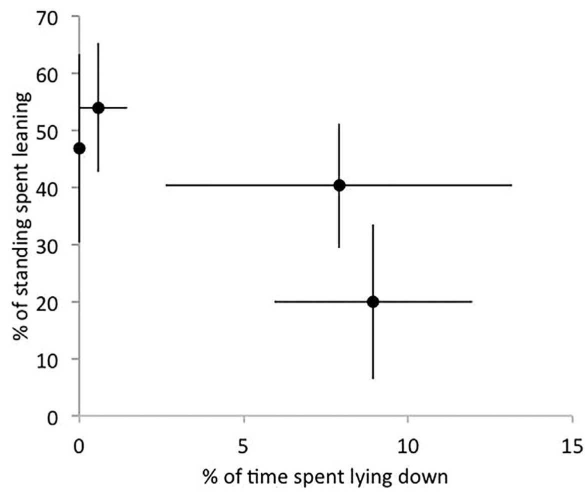
Statistical evaluations (summarized in Table 3) showed that in both elephant species, the time spent in lying rest decreases with age (Figures 1a and 1b). This also implies an increase in the time spent in standing rest in both species (Table 3); however, in Asian but not African elephants, the data nevertheless indicate a decrease in the total time spent resting with age (Figures 1c and 1d). In neither species is a laterality preference evident during lying rest (Figures 1e and 1f). In both species, there is a significant, inverse correlation between the time spent in lying and the time spent in standing rest (Figures 1g and 1h).

In Asian elephants, circus animals spent on average more time in lying rest than animals from zoos or orphanage, when corrected for age (statistics see legend of Figure 1b), whereas zoo elephants spent on average more time in standing rest (Figure 1d). For a given amount of lying rest, zoo animals spent more additional time in standing rest than zoo and orphanage elephants (Figure 1h).

Unfortunately, the literature data did not provide direct evidence that the standing rest that appears to compensate for the reduced lying rest is actually spent in a leaning position that might facilitate sleep. Therefore, we initiated a small observational study to address this question (Box 2).

BOX 2. Observations on correlation between lying and standing rest in zoo-kept female African elephants

In order to obtain further evidence whether leaning may be a substitute for lying, the first author conducted twelve 24 hr observations using the method of instantaneous scan sampling with a 5 min interval (Altmann, 1974) on a group of four female African elephants at Basel Zoo. The categorized resting (standing freely, standing with leaning, lying) behavior of each individual elephant was recorded and subsequently allowed the calculation of the daily percentage of time each elephant spent lying down, standing, or leaning. Due to the small sample size of four animals, data were only displayed graphically without statistical evaluation. Data of 12 complete 24 hr observation periods were collected with a percentage of 99.9 (13′811/13′824) successful scans, meaning that elephants were out of view in less than 0.1% of observation time. One animal (the same animal as in box 3) never lay down during the complete observation period. Data revealed the two elephants with longer lying durations to show less leaning behavior. The individuals that hardly ever lay down (<1% of time) compensated for that by extended leaning while standing.



Correlation between daily amount of lying and leaning while standing in a group of four female African elephants (*Loxodonta africana*) aged, from left to right, 45, 38, 21, and 21 years. Data represent means and standard deviations.

4 | DISCUSSION

The findings of the present study raise the question about the reason for unexpected falls in inactive and seemingly sleeping elephants, and suggest that a lack of lying or (safe) standing rest may be involved. This is particularly supported by a series of falling bouts in an older African elephant that were directly linked to the temporary lack of opportunities for leaning rest (Box 3).

While we cannot answer the question about the prevalence of falls in this study (and, given the absence of widespread video surveillance, this may remain unknown in the future), and the effect of potentially preventative measures has not been investigated so far, we intend to raise awareness and recruit the interested zoo community to evaluate the measures suggested here.

Due to common working hours in a zoo setting, with an absence of keepers during the night-time, and often with non-existent or incomplete camera recordings, sleep deprivation in zoo elephants might remain unrecognized for considerable time. The situation becomes acute when an elephant is recumbent and unable to get up again. The four documented cases, which occurred in European zoos during the past

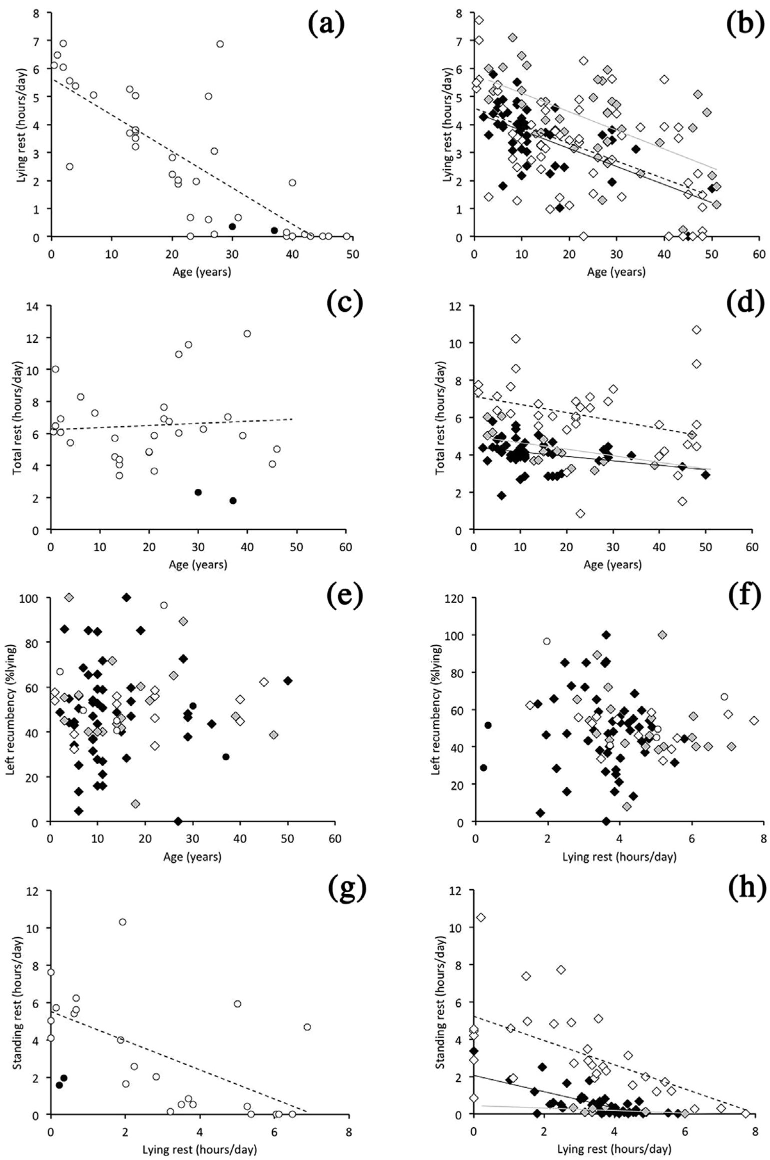


FIGURE 1 (a) Relationship between age and lying rest in zoo (open circles, dashed regression line) and free-ranging (closed circles) African elephants (*Loxodonta africana*); for statistics see Table 3). (b) Relationship between age and lying rest in zoo (open diamonds, dashed line), circus (gray diamonds, gray line), and orphanage (closed diamonds, black line) Asian elephants (*Elephas maximus*); a General Linear Model indicated both a significant effect of age [$F = 64.979$, $p < 0.001$] and of origin [$F = 12.239$, $p < 0.001$] on the time spent in lying rest, cf. also Table 3). (c) Relationship between age and total rest in zoo and free-ranging African elephants (no significant effect of age on the time spent in total rest cf. Table 3). (d) Relationship between age and total rest in zoo, circus, and orphanage Asian elephants (a General Linear Model indicated both a significant effect of age [$F = 10.462$, $p = 0.002$] and of origin [$F = 28.772$, $p < 0.001$] on the time spent in total rest, cf. also Table 3). (e) No effect of age or (f) time spent lying on the proportion of lying spent in left recumbency (for statistics see Table 3). (g) Relationship between lying rest and standing rest in zoo and free-ranging African elephants (for statistics see Table 3). (h) Relationship between lying rest and standing rest in zoo, circus, and orphanage Asian elephants (a General Linear Model indicated both a significant effect of lying [$F = 48.411$, $p < 0.001$] and of origin [$F = 42.936$, $p < 0.001$] on the time spent in standing rest, cf. also Table 3). Literature data (Björk, 2011; Boyle et al., 2015; Braidwood, 2013; Friend, 1999; Friend & Parker, 1999; Gebbing, 1959; Gravett et al., 2017; Ibler & Pankow, 2012; Kandler, 2010; Kurt, 1960; Kurt et al., 2001; Laws et al., 2007; Meller et al., 2007; Posta, Huber, & Moore, 2013; Rönnborn, 2014; Tobler, 1992; Walsh, 2017; Weisz et al., 2000; Williams et al., 2015; Wuestenhagen et al., 2000)

years, demonstrate a correlation with inadequate resting opportunities. We believe that these cases demonstrate that a state similar to “excessive drowsiness” of horses (Bertone, 2006) also occurs in elephants. Although the four elephants with a reported falling bout varied in age and health status, their case histories have in common a lack of lying rest over a time span of several weeks or even months. Additionally, no organic alterations (e.g., hematological parameters, infectious disease, injuries) explaining a sudden weakness were diagnosed in any of the individuals. Moreover, on the video documentations the elephants seemed to be completely unaware of the danger

BOX 3. Repeated collapse in a zoo-kept female African elephant, 44 years old

The cow had been suffering from chronic degenerative joint disease and stopped lying down completely in April 2015. In the morning of the 26th of October 2015, staff found the elephant cow recumbent on her left side. Video monitoring suggested that she had slept while standing. At around 5.30 am, she fell on her left side without premonitory signs or signs of preventative actions. Emergency treatment was initiated and within hours, staff succeeded in putting her back on her feet. Blood samples were taken, but biochemistry and hematology values were within reference ranges. Five similar bouts of falling occurred during the following weeks. Observations conducted during this period revealed extensive amounts of swaying, while feeding and standing rest activity in a leaning position dropped dramatically. After the transfer of the elephant group to their new exhibit on the 24th of December 2015, the old cow stopped nocturnal swaying immediately and returned to her usual activity pattern. Her osteoarthritis is under continuous medical treatment and her body condition has improved gradually. While the elephant had no access to such locations in the old house due to restrictions caused by the construction activity, she found specific positions in the new elephant house that allow her leaning during standing rest. Especially leaning against the horizontal bar of the gate seems appropriate for her to get a temporary relief of her limbs. Moreover, she makes use of the provided soft flooring (bark mulch) by standing/leaning there and propping up her head by sticking her long tusks into the soft ground.

Pictorial documentation of the female African elephant (*Loxodonta africana*). (a and b) Date and Body Condition Score (BCS) ascertained according to (Morfeld, Lehnhardt, Alligood, Bolling, & Brown, 2014; Wijeyamohan, Treiber, Schmitt, & Santiapillai, 2015). (a) 2015-03-18 BCS: 2/10 (b) 2016-12-13 BCS: 6/10. (c and d) During the leaning position in standing rest, the elephant tries to give weight to an appropriate structure on which she rests her hip joint/pelvis.

for a more detailed case description, see online supplementary S1

due to the drowsy state they were in, and falling came fully unexpected, as evidenced by both a lack of premonitory signs (such as trembling, swaying, or staggering) and a lack of signs of preventative reactions to the impeding fall (such as weight shifts or side steps). After hitting the ground, they showed signs of disorientation, such as looking around and moving slowly, before they tried to get up again. In the absence of more objective evidence, these videos appear to show animals that are asleep, fall down, wake up due to the fall, and (try to) get up again.

In two cases, degenerative joint disease might have caused reluctance to lay down, preventing the natural motion sequence of getting down and up again. Elephants in captivity are known to be prone to degenerative joint disorders in old age and subsequent avoidance of lying rest (Miller, Hogan, & Meehan, 2016; Roocroft, 2005). Whether this alteration in behavior is caused mainly by joint stiffness or pain alone might be hard to differentiate. Moreover, a decreased duration of lying with a shift to standing rest in lactating elephant cows and during late stage of pregnancy has been reported previously (Ibler & Pankow, 2012; Kurt, Garai, Reimers, & Schmidt, 2001). In mares late in gestation, reluctance to recumbent rest due to physical discomfort has been mentioned as well (Coomer & Fouché, 2010). In addition, previous research in captive elephants revealed reluctance of lying rest in situations where the animals do not feel completely safe (Laws et al., 2007; Roocroft, 2005; Williams, Bremner-Harrison, Harvey, Evison, & Yon, 2015). Investigating effects of an inter-zoo transfer of an adult Asian elephant bull, a significant change in resting behavior was reported (Laws et al., 2007). The observed elephant changed his sleeping behavior from 95% lying rest before transportation to 0% lying rest and 100% standing rest during his 10 first days at the new facility (Laws et al., 2007). A decrease in lying rest was also observed in a female African elephant after losing her conspecific (Koyama, Ueno, Eguchi, Uetake, & Tanaka, 2012).

Although causes for reluctance to lie down may vary considerably, the outcome with a sudden fall remains the same in the cases discussed here. Their history is strikingly similar to the two mentioned case reports in horses (Bertone, 2006).

Comparisons of literature data collected in extensively kept orphanage, zoo, and circus elephants might be misleading due to fundamentally different husbandry circumstances (e.g., chaining, working, and show schedule). Additionally, there is a close relationship between lying rest and age in elephants (see below), which means that

FIGURE 2 Soft interactive flooring provides elephants with various opportunities for lying rest. Piles and mounds facilitate the motion sequence of getting up and down. Note the standing female guarding the sleeping calves (©Dublin Zoo)

in comparing different elephant groups, their age structure needs to be considered.

Nevertheless, the following correlation patterns can be drawn from the findings in the literature: 1) With increasing age, duration of lying rest decreases in elephants of both species (Figures 1a and 1b). Younger, healthy, and comfortable-feeling elephants seem to prefer recumbent rest, while older, physically ailed, or stressed elephants avoid this position (Holdgate et al., 2016; Laws et al., 2007). Asian elephants appear to sleep longer in a recumbent position than African elephants, in particular older individuals. This finding corroborates the results of a recent study on zoo elephants in North America (Holdgate et al., 2016). 2) Zoo elephants show more extended daily rest compared to their counterparts from circuses, orphanages, or the wild (Figures 1c and 1d). This finding is in accordance with the results of the comparative study on elephants in North American zoos (Holdgate et al., 2016). 3) In general, elephants do not seem to have a side preference for lying rest, although individual preferences may exist (Gebbing, 1959; Kurt et al., 2001; Tobler, 1992; Weisz, Wuestenhagen, & Schwammer, 2000; Wuestenhagen et al., 2000) (Figures 1e and 1f). 4) The major time of resting in elephants is in the early hours of the morning (0.00–06.00 am) (Table 2). Most importantly, 5) in both captive and free-ranging elephants, resting behavior has been observed in a standing as well as a lying position, and there is an inverse correlation between lying and standing rest (Figures 1g and 1h), which supports the concept that standing rest can be a substitute for lying rest (Braidwood, 2013; Kurt et al., 2001; Laws et al., 2007).

In addition to sleep in standing and recumbent position, leaning behavior during bouts of standing rest has been repeatedly documented in free-ranging as well as captive elephants (Braidwood, 2013; McKay, 1973; Roocroft, 2005; Tobler, 1992; Wuestenhagen et al., 2000). Leaning elephants may successfully transmit weight to another object, which allows relief and relaxation of the anti-gravity musculature. The latter might enable a state of partial muscle atonia usually obtained during REM sleep (Gonfalone & Jha, 2015). Whether

FIGURE 3 Examples for captive elephants temporary relieving their limbs. (a) Placing foot on an elevated structure; (b and d) Resting trunk and tusks on an elevated structure; (c) Resting head on a horizontal structure; (d and e) Leaning against a solid item with a weight shift to one side; (f) Leaning against a solid item with a weight shift to the hind quarters (*Picture f*) © Klaus Rudloff)

FIGURE 4 Making use of its tusks to get a more relaxed sleeping position (resting and locking the head into the grid door) may lead to abrasions on the tusks of an elephant

elephants can enter REM sleep when leaning in a standing position remains to be investigated.

Although our observational data set is limited due to the small sample size, this finding supports the assumption that leaning rest may compensate for a lack of lying rest.

5 | PRACTICAL SOLUTIONS: HELPING ELEPHANTS TO SLEEP

If the aforementioned hypotheses concerning the individual elephant́s reluctance to lie down are correct, immediate treatment of the causing factors is rarely possible (Table 1). In order to manage these situations, two objectives should be followed: 1) the facilitation of lying rest, and if this is not feasible and 2) encouragement of safe standing rest. Concerning the latter, provision of appropriate environmental structures might encouraged special leaning positions.

5.1 | Facilitating lying rest

Considering lying rest as the optimal opportunity for elephants to enter REM sleep and thus an indicator for their welfare (Asher, Williams, &

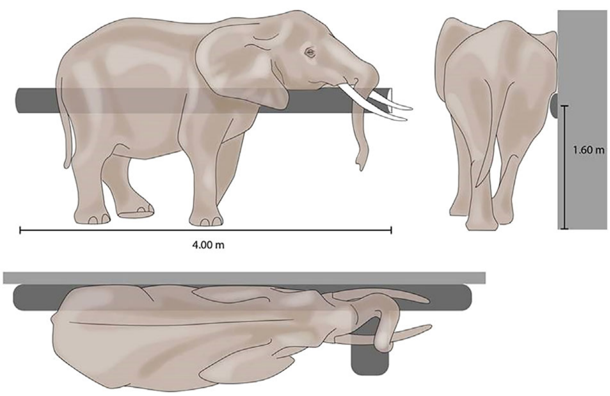


FIGURE 5 Drawing of a horizontal protuberance suggested to facilitate relaxed leaning behavior for an elephant (drawing by Jeanne Peter)

FIGURE 6 While vertically installed tree trunks are found commonly in elephant exhibits, horizontal ones are applied rarely

Yon, 2015), provision of an environment that allows this behavior is of highest priority. Quite often this can be achieved by the installation of soft flooring (e.g., sand, bark chips, bark mulch, or thick layers of straw), which allows the building of mounds (up to elephant height) and slopes (Roocroft, 2005; Williams et al., 2015) (Figure 2). The latter facilitate sleeping positions from which elephants can get up again with more ease, which is the critical aspect especially in physically handicapped individuals (Braidwood, 2013; Roocroft, 2005). Additionally, elephants which do not lie down due to vigilance, insecurity, or anxiety might rather take on an opportunity for lying rest if they know that they can get up quickly. Providing sufficient sleeping places for each individual of a group including a certain distance from each other is of high priority (Brockett, Stoinski, Black, Markowitz, & Maple, 1999). Otherwise, a subordinate elephant will not get access to the best possible substrate during resting time. Substrate choice will depend on the specific circumstances of an elephant-keeping institution. As a general recommendation, flooring should be soft and deformable. The latter aspect will also facilitate physical exercise and environmental enrichment (Roocroft, 2005). Sand appears as a useful substrate that can be shaped into mounds by the use of a small wheel loader.

5.2 | Facilitating safe standing rest

When quality and structure of substrate is not the causing factor for the lack of lying rest or installation of sand mounds is not feasible, elephants may benefit from peculiar adaptations in their environment that facilitate standing rest. How structures that support standing rest should be designed can be gleaned from elephant-specific standing rest behavior. Given the enormous body weight of an elephant, these animals look for ways to relieve their limbs during resting times. They reach this by either shifting weight away from the corresponding limb/body side, by leaning against a massive item, or positioning body parts (trunk, tusks, head, feet) on an appropriate environmental structure (Figure 3). Success in finding such a position depends mainly on the environment provided to the individual elephant. Consequently, if no ideal structure is available, an elephant might choose positions that lead to secondary pathologies (e.g., pressure ulcerations of the skin or tusk abrasion) (Figure 4). Looking at leaning positions more closely, it appears that elephants try not only to shift their body weight, but additionally to position their pelvis and/or hip joints on a protuberance if available (Figures c and d BOX 3). Moreover, they make use of environmental structures to place their trunk, tusk, head, or feet to get a temporary relief (Figure 3). In such a position, they seem to reach a level of relaxation, enabling extended resting phases (Wuestenhagen et al., 2000). On the basis of personal observations we suggest a diversity of environmental structures to be helpful for elephants, for example tree trunks, rocks, gates, poles, or ropes, to name a few.

Although identifying and treating the underlying cause would be ideal, immediate installation of appropriate devices is strongly recommended if an elephant stops lying rest, independent of whether this is a temporary or constant state. To allow resting the hip or pelvis, a protuberance should be installed in a horizontal direction on an appropriate individual level. Based on some measurements of items that were accepted for leaning against by elephants, benchmarks for the measurements of the protuberance are given (Figure 5), but any structures should be custom-fitted to the elephant they are offered to. Unfortunately, comparable horizontal structures occur rarely in elephant enclosures compared to vertical ones (Figure 6). Due to their availability and low costs, halved tree trunks, or wooden poles might be good options, if fixed on a wall. They can be replaced from time to time, depending on the interaction of the elephants with the structures in the same manner as already practiced for vertical trunks. Considering that elephants often lean against hard surfaces and even edges of steel bars, they might not require softer materials than wood. Optionally, parts of old tires might be added on the surface of the protuberance. Several studies have demonstrated extended periods of standing rest in elephants after provision of a softer ground (Braidwood, 2013; Meller, Croney, & Shepherdson, 2007). Thus, positioning the promontory in an area of the exhibit with soft ground substrate might increase the acceptance of a leaning device. Additionally, the location of the leaning device may be combined with a heating system inside the wall. Finally, it is important to offer sufficient amounts of leaning devices in regard to individual distance, rank, and social relationship.

6 | CONCLUSION

We report suspected excessive drowsiness in zoo elephants subsequently to recumbent sleep deprivation caused by variable factors. In each of the cases, the elephants' state led to an unexpected fall out of a standing position. In two cases, adaptations in the environment and management led to an uneventful recovery, and the other two elephants recovered spontaneously. Nocturnal video monitoring was critical in determining causal aspects and revealing opportunities for adaptations. Thus, our findings strongly underline recommendations for this kind of monitoring in any elephant-keeping facility (Walter, 2010). Actually, without video monitoring, falling bouts that do not result in permanent recumbency (as in three of the four elephants of the present study) might go unnoticed, so that in theory, there might be a relevant number of unrecognized cases.

Factors making an elephant reluctant to lie down were compiled from the current literature, and being aware of them will enable zoos to prevent recumbent sleep deprivation in their elephants. In cases where lying rest is not achievable, standing rest can be facilitated by the provision of horizontal structures that allow leaning behavior. A precise description how these might be practically constructed is provided and will hopefully support further improvement of zoo elephant welfare by allowing them satisfying rest at any point of life.

In order to draw reliable recommendations on the amount of sleep an elephant requires, further knowledge on position-dependence of sleep quality in elephants is needed. Although elephants and herbivores in general are supposed to enter deep sleep (REM-mode) only in a lying position, investigations based on electro encephalograms would be required to confirm this (Gonfalone & Jha, 2015; Gravett et al., 2017). Unfortunately, this technique is inappropriate for elephant anatomy with a relatively small brain inside a massive skull, and has not been adapted for the species yet (Gravett et al., 2017; Manger, Pillay, Maseko, Bhagwandin, & Gravett, 2009). However, Hatt and Martin Jurado (2011) reported a successful reading of brain activity with bispectral index in an awake Asian elephant by applying the sensors onto the skin. Whether this method might serve as a reliable tool to differentiate sleep modes in elephants needs further investigation.

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CONFLICTS OF INTEREST

None.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Unexpected Resting Behaviour in a Geriatric Zoo Elephant

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In der Folge meines Besuches im Longleat Safari Park, UK erhielt ich eine Anfrage zur Erarbeitung eines umfassenden Assessments des dortigen Asiatischen Elefanten. Dieser Auftrag konnte zwischen November 2016 und August 2017 erfüllt werden. Die Beobachtungen zum Schlafverhalten dieses geriatrischen Elefanten sollen veröffentlicht werden.

Short Communication Gajah 48 (2018) 30-33

Unexpected Resting Behaviour in a Geriatric Zoo Elephant

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Introduction

Although observational data on natural resting behaviour in free-ranging Asian elephants (*Elephas maximus*) are lacking, lying rest is considered essential and may be used as a welfare indicator under captive conditions (Asher *et al*. 2015). Actual requirements of lying rest in elephants have not been determined, but the expression of this behaviour seems to decrease with age (Fig. 1a). Due to impaired musculoskeletal strength and degenerative joint disease, geriatric elephants are often observed to avoid lying rest completely (Wuestenhagen *et al*. 2000; Roocroft 2005; Kandler 2010; Braidwood 2013). Instead, they express a higher amount of standing rest possibly as a substitute for lying rest (Fig. 1b).

Considering the scarcity of quantitative data, each additional case report may enhance our understanding of restorative sleeping behaviour in elephants. Within the scope of a welfare assessment, we were able to investigate the nocturnal resting behaviour of a geriatric zoo elephant. It was the aim of our observations to quantitatively evaluate this individual's resting behaviour.

Material and methods

The subject of our study was a female Asian elephant born in Sri Lanka in 1952 and living in a Safari Park in the UK (van Wees & Damen 2016). Before this single kept elephant was moved to her current location in 2011, she had travelled with a performing circus for more than 50 years without any contact to further elephants during the last 20 years (Ellicott 2016). Due to the elephant's age and presumed severe arthritis mainly in both knee joints, it was decided not to bring another elephant in (Ellicott 2016). The elephant shares her exhibit, consisting of a sand-floored indoor and a greened outdoor exhibit, with three Anglo-Nubian goats. During observation nights, access was mostly restricted to the indoor area due to low ambient temperatures.

A video monitoring system was in place and provided data for our observations. Indirect observation by camera recordings was conducted between the 27th of November 2016 and the 19th of April 2017 for a total of 20 nights (18:00–8:00). Observations took place on a cluster of consecutive nights (on average 6.67 ± 4.16 nights) with several weeks between such clusters. Data were collected by continuous sampling (Altmann 1974) accurate to the minute. Lying rest was defined as lying motionless on the ground in a recumbent position. For each lying bout, the side on which the elephant lay was recorded. Total duration of lying rest was calculated for each night, as well as the average duration of lying bouts.

Results

On the video recordings the elephant was visible at all times and image quality allowed unambiguous identification of the behaviour. The elephant had one or two bouts of lying rest during each night, ranging in duration between 50 and 535 minutes. In total, 30 bouts of lying rest were observed with a mean duration of 314.3 ± 152.3 minutes. In 15 bouts the elephant chose her left side to lie on, i.e. exactly 50% of

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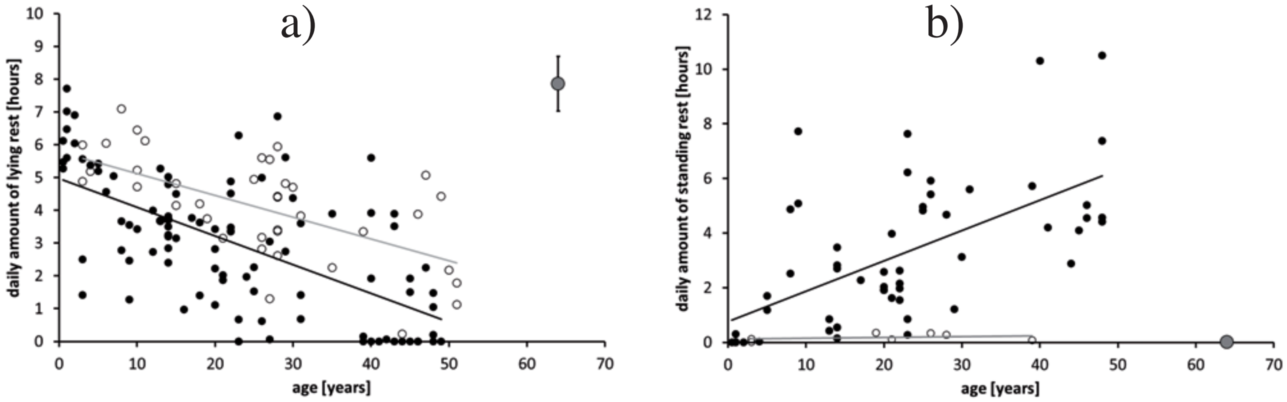

Figure 1. Correlation between daily amount of (a) lying and (b) standing rest and age in circus (circles and regression line in grey) and zoo (filled circles and regression line in black) elephants (*Elephas maximus* and *Loxodonta africana*) and the outstanding position of the observed elephant (grey circle) (literature data reviewed in Schiffmann *et al*. (2018)).

the cases (Table 1). On average the animal slept for 471.6 ± 49.9 minutes each night. She had her lying rest exclusively on the moderate slopes of sand piles provided in her indoor exhibit (Fig. 2). The majority of the elephant's lying rest activity occurred between 21:00 and 7:00 (Table 1).

According to her keepers, very short lying or leaning bouts during daytime (8:00–18.00) were observed on rare occasions. During the study period no measurable time of inactively standing still, which might be classified standing rest, occurred (see also Fig. 1b).

Discussion

Although quantitative data regarding lying rest in Asian elephants are scarce and restricted to observations under captive conditions, its duration seems to decrease with increasing age (Fig. 1a). According to her year of birth indicated in the EEP-studbook, the observed female is one of the oldest elephants living in Europe (van Wees & Damen 2016). Thus, very short bouts or even absence of lying rest was expected, especially with respect to the elephant's reduced mobility due to severe arthritis. Under these premises, the extended bouts of lying rest documented here were completely unexpected. To date, no comparable amount of lying rest has been reported in elderly zoo elephants in either species (Fig. 1a).

The absence of a side preference for lying rest corroborates findings reported in the literature (Gebbing 1959; Kurt 1960; Tobler 1992; Weisz *et al*. 2000; Wuestenhagen *et al*. 2000; Laws *et al*. 2007; Kandler 2010), as does the expression of major sleeping activity in the early hours of the morning (Kurt 1960; Tobler 1992; Friend 1999; Friend & Parker 1999; Weisz *et al*. 2000; Wuestenhagen *et al*. 2000; Kandler 2010; Ibler & Pankow 2012; Boyle *et al*. 2015; Williams *et al*. 2015; Holdgate *et al*. 2016). However, the female observed here expressed an additional peak of lying rest between 21:00 and midnight (Table 1).

It can only be speculated which factors led to the extensive lying resting behaviour in the observed elephant. Sand-flooring with slopes and mounds represents a key factor to facilitate lying rest in elephants (Roocroft 2005; Holdgate *et al*. 2016; Walsh 2017). Thus the observed pattern may be related to the availability of such features in the enclosure. Extended lying bouts might also be explained by a desire to avoid getting up

Figure 2. The elephant exclusively chose the slopes of sand piles for lying rest.

Table 1. Compilation of 30 bouts of lying rest observed during 20 nights (18:00–8.00).

Night	Lying side	Time start	Time end	Rest per bout [min]	Total rest per night [min]
1	right	21:24	5:34	490	490
2	right	20:31	5:11	520	520
3	left	21:25	23:08	103	440
	right	0:21	5:58	337	
4	left	20:08	22:27	139	526
	right	0:07	6:34	387	
5	left	20:59	0:38	219	545
	right	1:42	7:08	326	
6	right	22:22	5:37	435	435
7	left	21:03	23:06	123	437
	left	0:16	5:30	314	
8	right	21:28	5:25	477	477
9	left	22:36	23:38	62	408
	right	0:46	6:29	344	
10	right	21:32	6:01	509	509
11	right	21:30	0:45	195	457
	left	2:58	7:20	262	
12	left	23:43	6:30	407	407
13	left	22:16	7:11	535	535
14	left	22:35	0:25	110	451
	right	1:32	7:13	341	
15	right	21:52	3:27	335	496
	left	4:00	6:41	161	
16	left	22:47	7:01	494	494
17	right	22:13	6:41	508	508
18	left	22:16	23:06	50	349
	left	2:07	7:06	299	
19	right	22:18	6:33	495	495
20	left	22:14	2:01	227	452
	right	2:41	6:26	225	

and down, due to musculoskeletal alterations, although this is generally considered to cause the opposite behaviour of not lying down at all (Wuestenhagen *et al*. 2000; Roocroft 2005; Kandler 2010; Braidwood 2013). The observed female did not show evidence of problems getting back up after rest: From her lying position on the sand pile, she easily changed to sternal recumbency, pushed herself up on her front legs, and then the hind legs.

Analysis of data from the literature revealed increased lying behaviour in circus compared to zoo elephants (Benedict 1936; Gebbing 1959; Kurt 1960; Friend 1999; Friend & Parker 1999) (Fig. 1a; Schiffmann *et al*. 2018) possibly related to the structured daily routine of circus life. Although, having lived for many years at a circus, this alone might not explain the outstanding resting behaviour of this elephant. The observed pattern might rather be considered an idiosyncratic behaviour of this individual. Alternatively it can be speculated whether geriatric elephants would usually express such an extended lying rest if they were provided with a more conducive environment. Unfortunately quantitative data on lying rest in free-ranging Asian elephants is lacking as well as data for captive individuals of a similar age (reviewed in Schiffmann *et al*. 2018). Whatever the reason, extended daily lying bouts with complete weight relief of all four limbs are likely to be highly beneficial for an elephant suffering severe degenerative joint disease.

In conclusion, this case report provides evidence of extended bouts of lying rest in a geriatric zoo elephant. We consider this behaviour beneficial for an elephant's well-being and health. Installation of malleable sand-flooring for captive elephants may encourage lying rest and is strongly recommended.

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Impact of a new exhibit on stereotypic behavior in an elderly captive African Elephant

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Der Zoo Basel unterstützte mein Dissertationsprojekt von Beginn an. Durch den Kontakt zum damaligen Zootierarzt bot sich die Gelegenheit zur Dokumentation des Einflusses der neuen Basler Elefantenanlage auf das stereotype Verhalten eines älteren Tieres. Die Erkenntnisse sollen der Öffentlichkeit zugänglich gemacht werden.

Impact of a new exhibit on stereotypic behavior in an elderly captive African elephant

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Abstract

Stereotypic behavior in zoo elephants is considered an indicator of impaired welfare. The underlying causes are diverse and many aspects are still unexplored. Nevertheless, many zoological institutions take huge efforts to improve the well-being of their elephants. The construction of a new exhibit provides a chance to gain further evidence on the impact of such measures on elephant behavior. We report a significant decrease in the amount and frequency of swaying in an elderly African elephant (*Loxodonta africana*) after transition to a new enclosure. While we assume that continuous social interactions, increased freedom of choice and appropriate resting locations were critical for the distinct improvement of this individual´s well-being, the only factor that significantly correlated with swaying in this individual was the amount of time per day the elephant group was separated. These factors are in large part independent of enclosure size. Thus, corresponding adaptations in elephant husbandry are also encouraged in facilities without resources for the building of extensive new exhibits and may lead to increased zoo elephant welfare.

Introduction

Stereotypical behavior especially in the manner of swaying is quite common in captive elephants (Greco et al., 2017; Greco et al., 2016). Stereotyping is generally defined as functionless repetitive behavior, independent of the underlying cause and situation of its occurrence (Mason, 1991; Mason and Veasey, 2010). This unnatural repetitive behavior has been documented in semi-captive elephants living in countries of origin as well as in North American and European zoos (Clubb and Mason, 2002; Greco et al., 2016; Kurt and Garai, 2001). In extreme cases elephants have been reported to spend up to 66% of their time in stereotypic behaviors (Kurt and Garai, 2001; Meller et al., 2007). Nevertheless, little research has been conducted on the causal factors of this behavior yet (Greco et al., 2017). Correlation with indicators of stress and poor health have been confirmed (Haspeslagh et al., 2013; Kurt and Garai, 2001) and stereotypic behavior is widely considered as a sign of impaired welfare (Asher et al., 2015; Mason and Veasey, 2010).

Targeting a further improvement of elephant management and care, modern zoos take huge efforts in rebuilding enlarged enclosures and optimization of husbandry methods. Ideally, these actions lead to an increase in natural behavior, while unnatural behaviors including stereotyping decrease (Soltis and Brown, 2010). Looking at the scarcity of evidence by specific reports (Braidwood, 2013; Jacobs, 2011; Lucas and Stanyon, 2016), uncertainties concerning the expectable effects of a new exhibit on stereotypic behavior of an elephant remain. Thus, every single observation may enhance our knowledge in this subject. This case report aims to (I) document changes in the amount of swaying in an elderly female African elephant (*Loxodonta africana*) during and after the reconstruction of a new elephant exhibit at Zoo Basel. Additionally, (II) potential influencing factors were assessed to identify parameters that might be most critical. Ideally, consideration of these parameters may provide further helpful advice to elephant-keeping facilities in optimizing their husbandry conditions.

Material and methods

Site and subjects

The study was conducted at Zoo Basel, Switzerland from April 2015 until September 2017. The observations covered the construction process of a new elephant exhibit and the transfer of the elephant group to their new environment. Relevant features of the old and new elephant exhibit, which was constructed on the area of the old exhibit, are summarized in Table 1 and impressions shown in Figure 1. The main goal of the new exhibit in terms of elephant husbandry was the facilitation of natural elephant behavior with diversified feeding, locomotion and social interactions (Hoby and Baumeyer, 2017). Moreover, the conception of the new elephant enclosure was to provide free access to various indoor and outdoor areas whenever weather conditions allowed it, and to stop separation of females during nighttime and thus encourage cohesion between the elephants (Hoby and Baumeyer, 2017). Although it was intended to establish a breeding group, the new bull elephant arrived only in May 2017 due to a lack of space during the construction period. Subject of the observation was a group of four unrelated female African elephants (*Loxodonta africana*) ranging in age from 20 to 44 years. The two younger females are assumed to originate from the same herd and to have a degree of kinship (Hüppi, 2014). Focus was laid on the oldest elephant in the group. This peculiar elephant is supposed to have been wild-born in Tanzania in 1971. Before her arrival at Zoo Basel on the 30th of November 1984, she lived in a Swiss Circus since her importation in 1974. Several years after her transfer to the zoo, she became pregnant and had a stillbirth of a mature calf in 1992. She had no further pregnancy since then. With an inter-institutional transfer, unsuccessful breeding and as a member of a non-breeding group of mainly unrelated females, the elephant´s history and current situation contained several factors reported to increase the chance for the occurrence of stereotypic behavior (Greco et al., 2016). According to the elephant keepers, the female elephant showed regular swaying since her arrival at Zoo Basel in 1984, whereas the other herd mates did not show any stereotypic behavior.

Data collection

According to the different steps of reconstruction, data collection was divided into five observation periods. Detailed information on the circumstances during the different periods is given in Table 2. During each period, three full days (24 hours) of observation (all performed by the first author) were conducted with an interruption of 3 to 21 days. This approach resulted in a total observation time of 72 hours per period. A camera system was not permanently in place and could not guarantee visualization of every elephant at every point of time. Data were collected by instantaneous scan sampling with an interval of 5 minutes (min) (Altmann, 1974). An ethogram consisting of 9 categories (see Appendix) was applied and the observed category manually noted on a data sheet. Additionally, stereotypic behavior and lying rest were recorded by continuous sampling accurate to the minute (Altmann, 1974). The end of a stereotyping bout was noted if the elephant stopped swaying for at least 30 seconds. If two activities (e.g. foraging and walking) occurred simultaneously, the more dominant one was recorded. Moreover, moments of management actions like feeding, closing/opening of gates and interaction with keepers were recorded. Ambient temperature data for the observation days were extracted from an online resource http://www.klimabasel.ch/daten.htm (access on the 07.12.2017).

Statistics

Data were generally not normally distributed (as assessed by Kolmogorov-Smirniov-test), and therefore, nonparametric statistics were used. Correlations between various behaviours were assessed by Spearman's correlation coefficient, and differences between observation periods were assessed by Kruskal-Wallis-test. Additionally, in order to assess the two factors considered most influential for swaying (the time the group members were separated, and the time access was confined to specific parts of the enclosure), a General Linear Model was used (with residuals showing a normal distribution) with the proportion of time spent stereotyping as the dependent variable, and the time with access to all enclosure components (indoor and outdoor) and the time the whole group was allowed together as independent variables. The level of significance was set at a P-value <0.05.

Results

Instantaneous scan sampling during the 5 observation periods (15x 24 hours) resulted in a total of 4´310 successful scans out of 4´320 possible scans for the focus elephant. This means a success rate of 99.77%. During observations, a total of 192 swaying bouts were recorded with a total duration of 3´708 min (mean 19.3 min, SD ± 26.2 min, median 5 min, range 1-126 min) and a daily average of 247.2 min, (SD ± 304.0 min, median 201 min, range 0-990 min) (Table 3). The latter corresponds to an amount of 17.17% of the total observation time. The female elephant showed stereotypic behavior exclusively in the form of stationary whole-body movements from side to side, which was described as swaying or weaving (Greco et al., 2017). Supplemental material provides a video sequence of this behavior (Video S1). The number of bouts and daily duration of swaying varied between the different observation periods (Fig. 2). Highest values were recorded in period 2, and lowest in periods 3 and 5, respectively (Fig. 2). On the last day of observation (day 15) not a single bout of swaying was recorded. Differences in the proportion of time spent swaying differed significantly between the five periods (P = 0.043). The focus elephant showed swaying exclusively during periods, when access was restricted to either the outdoor or indoor area, independent of observation period and area available. No single bout of swaying was recorded when the elephants had access to both the indoor and outdoor area (Table 3). The other behaviors for which a significant difference between the observation periods were found were feeding (P = 0.039) and leaning while resting (P = 0.047).

The proportion of time spent swaying was significantly negatively correlated in the elephant to the time spent resting, time spent feeding, and time spent in locomotion (Fig. 3a, Table 4). Differentiating the resting behavior in more detail, the negative correlation was evident with leaning, but not with free-standing behaviour (Fig. 3b, Table 4). Among the potential contributing factors to stereotyping, temperature showed no significant correlation (Table 5). There was a significant negative correlation between the time all elephants were allowed together and the time spent stereotyping (Fig. 3c, Table 5), but no correlation with the time that all enclosure areas were accessible for the animals (Fig. 3d, Table 5). Correspondingly, in the General Linear Model (F = 38.274, P < 0.001, adj. R^2 = 0.84), time with access to all enclosure areas was not significant (F = 0.169, P = 0.688), whereas time when all animals were allowed together was (F = 64.596, P < 0.001).

Discussion

Application of our simple ethogram allowed unambiguous categorization of the elephant´s behavior during data collection. Simultaneous occurrence of two behaviors was rare and when it occurred, it was clear which behavior was dominant. Nevertheless, this decision contained a certain subjectivity by the observer. When observing directly, an influence of the observer´s presence on the elephant´s behavior can never be ruled out. In our case the elephants showed at most little notice and seemed to accept the presence of the passive observer quickly. Thus, we assume no significant influence on their behavior patterns.

Our method led to an extraordinary rate of successful scans (99.77%) which was distinctively higher than comparable recent studies with elephants categorized “out of sight” for at least 25% of time (Boyle et al., 2015; Williams et al., 2015). The female elephant expressed one single form of stereotypic behavior (swaying from side to side), which is reported to be the usual case in elephants with only a minority of them showing different patterns (Greco et al., 2017). Expressing swaying on average for 17.17% of time, the amount of stereotyping was in the middle of the range reported for zoo elephants (Björk, 2011; Braidwood, 2013; Elzanowski and Sergiel, 2006; Greco et al., 2017; Greco et al., 2016; Meller et al., 2007; Rees, 2009; Schmid et al., 2001; Stoinski, 2000; Wilson et al., 2004), although African elephants are generally considered to express less stereotypies than their Asian counterparts (Greco et al., 2016).

The amount of swaying in our focus elephant varied between the days and periods of observation and showed a distinct decline after period 2 (Fig. 2). This change correlated with the transfer of the elephant group to the new indoor exhibit, allowing the group to stay together during night- and daytime. After this period, the amount of daily swaying remained on a comparable low level during periods 3, 4 and 5 (on average 72.8 minutes ± 86.98; 5.06%). A similar decrease in stereotypic behavior after transition to an exhibit providing increased enrichment and choice to the elephants was reported for Blair Drummond Safari Park in Scotland (Braidwood, 2013; Jacobs, 2011; Lucas and Stanyon, 2016) .

Based on our data we could not detect any significant correlation between the elephant´s amount of swaying and ambient temperature (Table 5), which has been previously reported for the Asian species (Rees, 2004). In the latter report, the author considered temperature as compounding rather than causing factor for the occurrence of stereotyping. Thus, in the case of our focus elephant, changes in the amount of swaying might mainly be caused by more influential factors than ambient temperature. Because this case report does not represent an experiment with a controlled manipulation of a specific factor, we cannot pinpoint a single one, even if the statistical correlations indicate that the immediate deprivation of the habitual social contact was particularly decisive in the present case.

One important characteristic of the new exhibit at Zoo Basel is the extended feeding enrichment program. Reduction of stereotypic behavior in Asian elephants through extra feed supply with a higher feeding frequency has been demonstrated previously, although the effect was not consistent between individual elephants (Björk, 2011; Rees, 2009). Thus, reduction in swaying since living in the new environment could be explained by a more diversified feeding system. This hypothesis could not be confirmed by the development of the elephant's activity budget over the five periods of observation. A continuous decline of the percentage of time spent foraging occurred in periods 3 to 5 (Fig. 2). At the same time, the amount of time spent in a leaning position steadily increased (Fig. 2). According to the elephant keepers, the female had stopped having lying rest in April 2015 presumably due to degenerative joint disease. Subsequently she suffered several bouts of falling with the need of assistance to get up again between the 26th October 2015 and the 7th of January 2016 (Schiffmann et al., in prep.). This episode coincided accurately with the lowest amounts of leaning and foraging in period 2, with a peak in stereotypical behavior (Fig. 2). Assuming lying rest a positive and stereotyping a negative welfare indicator (Asher et al., 2015), this inverse correlation seems logical. If leaning behavior functions as a substitute for lying rest (Schiffmann et al., in prep.), increasing this behavior might lead to an improved well-being and thus reduce stereotypic behavior. During period 2 with highest percentage of swaying, the elephant showed a significant reduction in foraging (Fig. 2). This is in accordance with Kurt and Garai (2001) and Koyama et al. (2012) that observed intense stereotypic behavior to displace natural behaviors in captive elephants. Considering foraging and resting as natural behaviors, their negative correlation with the amount of swaying (Fig. 3) as well as the positive correlation between them (Fig. 3a) corroborates the aforementioned reports.

Having a closer look at the circumstances during period 2 provides explanations for the elephant´s behavior. During this period the group was constantly confined indoors for the nighttime and separated into two pairs. Separation and restricted access to indoor or outdoor area have both been identified as risk factors for stereotypic behavior in zoo elephants by Greco et al. (2016). Additionally, the elephant´s preferred location for leaning while indoors, a narrow walkway, became unavailable due to the progress of the construction site. An accumulation of these factors is supposed to be causal for the intense swaying during this period. It can be discussed, whether her falling bouts had a cause or effect relation with the excessive stereotypic behavior during these months. After transferring the elephants to the new indoor exhibit, the aforementioned risk factors were eliminated and unlimited social contact allowed. GLM analysis revealed the latter as single significantly correlating factor for the amount of stereotyping (Table 5), which is in accordance with previous reports suggesting social circumstances to have strongest impact on stereotypic behavior in captive elephants (Greco et al., 2016; Kurt and Garai, 2001; Vanitha et al., 2016). Kurt and Garai (2001) as well as Vanitha et al. (2016) investigated stereotypic behavior in captive elephants in countries of origin and suggest it a symptom of social isolation. This is in accordance with Greco et al. (2016), who´s models for North American zoo elephants revealed the social environment as most influential factor in predicting stereotypic behavior rates. Moreover, the new exhibit provides the elephants with increased spatial choice by free access to the indoor and outdoor area. In addition the elephant detected opportunities to have leaning rest in her new environment during the following months (Schiffmann et al., in prep.), which may have further increased her well-being. Due to the fact that swaying dropped already before the change from direct to protected contact (after observation period 3), the impact of the management on the behaviour may have been negligible.

In conclusion, we were able to document the amount of stereotypic swaying behavior in an elderly female African elephant during reconstruction of and transfer to a new enclosure (I). After allowing access to the new indoor area, the amount of swaying dropped dramatically. Permanent social interactions without any separation of the female elephant group, increased freedom of choice with access to indoor and outdoor areas as well as provision of locations for leaning rest were considered the critical factors for this reduction (II). Based on these findings, we assume social factors and complexity of an enclosure providing appropriate resting locations to be more relevant for the decrease of zoo elephant´s stereotypic behavior than exhibit size and dietary enrichment. Implementation of these aspects may allow immediate and significant improvement of elephant welfare in other facilities where construction of new exhibits or a spatial expansion of existing ones is not feasible.

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Table 1 Comparison of technical data from the old and new African elephant exhibit at Zoo Basel

Feature	Old exhibit (1952 – 2015)	New exhibit (opened in March 2017)
Outdoor area bull [m²]	450	1´010
Outdoor area cows [m²]	1´300	3´283
Indoor area bull [m²]	36.2	289
Indoor area cows [m²]	188	671
Total area [m²]	1´974.2	5´253
Management system	Free contact (females), Protected contact (male, since 02.08.1984)	Protected contact (females and male) since 03.08.2016

Table 2 Overview on the time frame, exhibit availability and husbandry characteristics during the five observation periods

Period of observation	Time frame	Exhibit available	Social conditions	Further remarks
1	03.04. – 25.04.2015	Old exhibit indoor and outdoor. Gates closed during the night on day 1 and open on days 2+3.	Elephants separated into two pairs when confined to the indoor area.	Free contact
2	11.12. – 23.12.2015	Old exhibit indoor, new male exhibit outdoor. Gates closed during the night.	Elephants separated into two pairs when confined to the indoor area.	Free contact
3	24.02. – 24.03.2016	New male exhibit indoor and outdoor. Gates closed during the night.	Elephants separated only for training sessions and individual feeding.	Free contact
4	05.04. – 28.04.2017	New exhibit indoor and outdoor. Gates closed during the night.	Elephants separated only for training sessions and individual feeding.	Protected contact
5	19.08. – 10.09.2017	New exhibit indoor and outdoor. Gates open during the night.	Elephants separated only for training sessions and individual feeding. Male irregularly with the herd, depending on sexual cycle of the females.	Protected contact

Table 3 Detailed data on a female African elephant´s (44) stereotypical swaying behavior during 15 days (24 hours) of observation

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11	Day 12	Day 13	Day 14	Day 15
bouts per day	27	11	12	39	22	18	4	5	6	11	12	6	15	4	0
average duration per bout [min.]	14.89	13	15	25.38	26.82	41.56	1.75	1.6	41.17	13.27	5.25	3.17	9.67	5	0
total duration per day [min.]	402	143	180	990	590	748	7	8	247	146	63	19	145	20	0
total duration while free access indoor + outdoor [min.]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
time of confinement to the indoor exhibit [min.]	1022	31	98	1205	1049	1083	1239	1233	1107	993	1076	1189	117	168	192
time of confinement to the outdoor exhibit [min.]	228	500	443	235	391	357	201	207	293	447	364	82	398	398	266
time with free access to the indoor and outdoor exhibit [min.]	190	909	899	0	0	0	0	0	40	0	0	169	925	874	982
time of separation of the group [min.]	1022	31	98	1205	1049	1083	38	7	19	44	14	13	55	0	86
average ambient temperature [°C]*	5.8	14.9	14.4	3.9	6.9	7.6	2.2	3.7	6.0	11.3	13.4	3.9	18.0	24.3	13.5

*data for ambient temperature were taken from the online resource http://www.klimabasel.ch/daten.htm (access on the 07.12.2017)

Table 4 Correlations between various behaviors of a female African elephant assessed by Spearman's correlation coefficient

	Feeding	Resting (total)	Resting (standing)	Resting (leaning)	Locomotion
Stereotyping	**R = -0.76** **P = 0.001**	**R = -0.82** **P > 0.001**	R = -0.13 P = 0.657	**R = -0.62** **P = 0.013**	**R = -0.56** **P = 0.028**
Feeding	-	R = 0.42 P = 0.120	R = -0.14 P = 0.629	*R = 0.48* *P = 0.073*	R = 0.43 P = 0.109
Resting (standing)	-	R = 0.43 P = 0.114	-	R = -0.47 P = 0.076	R = -0.32 P = 0.247
Resting (leaning)	-	*R = 0.51* *P = 0.052*	-	-	**R = 0.79** **P = 0.001**

Table 5 Correlations of the factors considered most influential for Stereotyping in a female African elephant assessed by Spearman's correlation coefficient

	Temperature	Time whole group allowed together	Time of access to all enclosure areas
Stereotyping	R = -0.01 P = 0.967	**R = -0.71** **P = 0.003**	R = -0.24 P = 0.394
Temperature	-	R = 0.07 P = 0.800	**R = 0.64** **P = 0.011**
Time whole group allowed together	-	-	R = 0.12 P = 0.659

Figure 1 Comparison of the old and new African elephant exhibit at Zoo Basel. Old indoor (a) and outdoor (b) exhibit during the first period of observation and both areas of the new exhibit (c,d) during period 4 and 5 of observation.

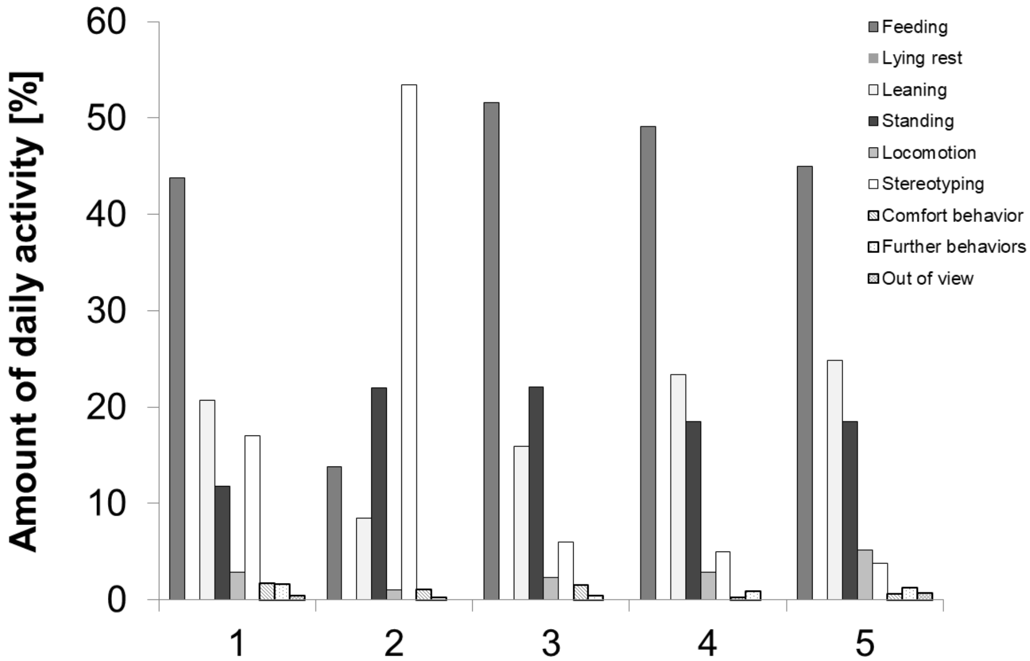

Figure 2 Activity budgets of a female African elephant during the five periods of observation

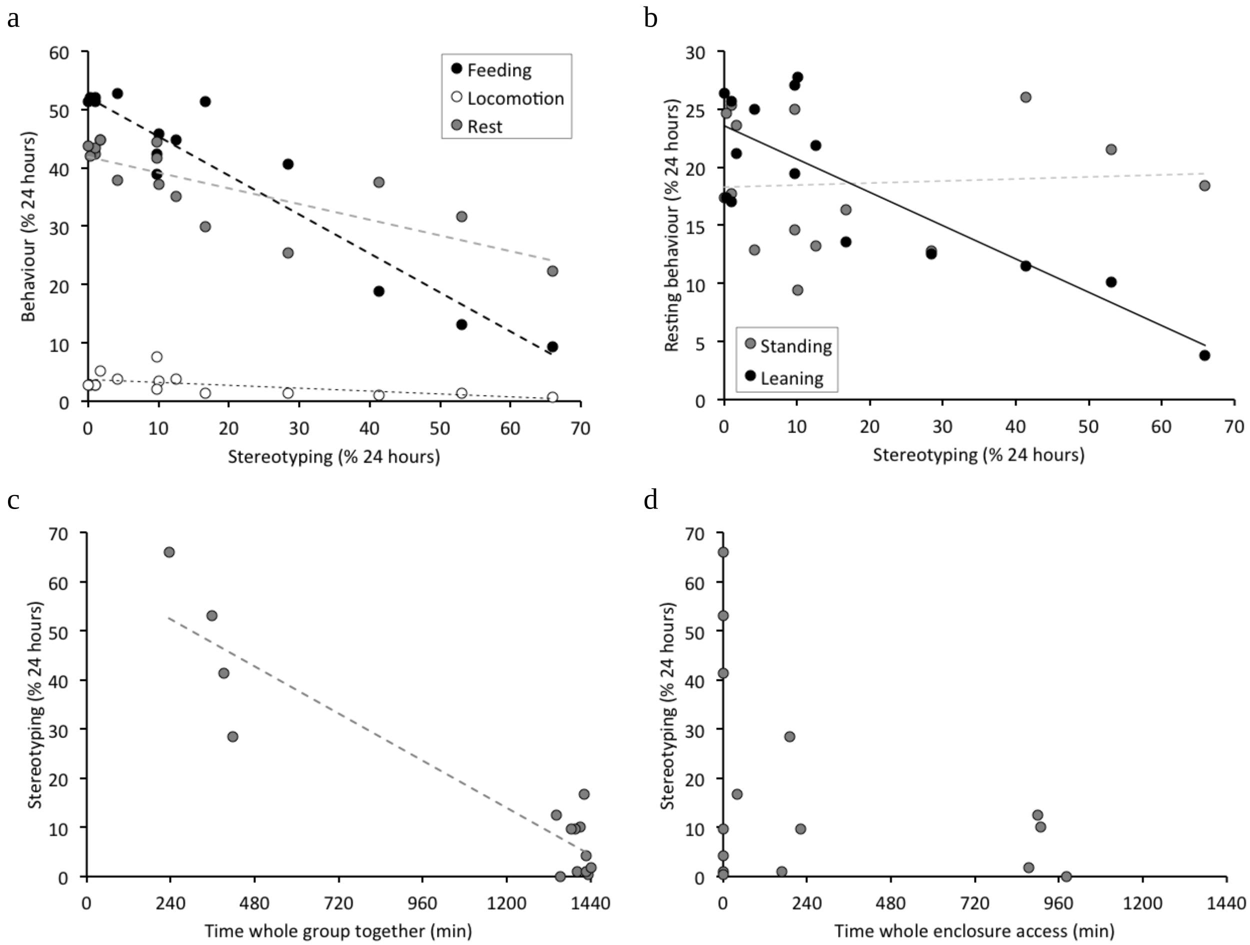

Figure 3 Correlation of daily stereotyping in a female African elephant with further behavior categories (a), resting behavior (b), separation of the group (c) and access to whole enclosure (d).

Appendix

Ethogram activity budget		
1	Feeding/Drinking	Activity for preparing and intake of feed as well as drinking
2	Lying rest	Position without any weight on all four legs and most part of the body has contact to the ground
3	Leaning	Standing in upright position with giving weight to an external object e.g. wall or rock
4	Standing	Standing in upright position without any recognizable activity
5	Locomotion	Spatial movement of more than ½ body length without any other activity
6	Stereotyping	Direction- and purposeless, repetitive behavior e.g. weaving, pacing, head bobbing
7	Comfort behaviors	rubbing, wallowing, powdering, bathing
8	Other behaviors	Tactile interaction with conspecifics or keepers, defecation, urination
9	Out of sight	Out of view, behavior cannot be determined

Modified from Wilson et al. (2006)

Seasonality of reproduction in Asian elephants *Elephas maximus* and African elephants *Loxodonta africana*: underlying photoperiodic cueing?

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Da gleichzeitig und an derselben Fakultät durchgeführt, bot sich eine unterstützende Beteiligung meinerseits bei der Forschung von Rahel Hufenus zur Saisonalität der Reproduktion bei Elefanten an. Bei der Veröffentlichung wurde ein von mir aufgenommenes Bilddokument für die Titelseite der Ausgabe gewählt.

Cover image: an Asian elephant *Elephas maximus* mother and her daughter in Zurich Zoo, Switzerland in April 2017. Second-generation breeding has been successful at this facility (see p. 261).
Photo: Christian Schiffmann.

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REVIEW

Seasonality of reproduction in Asian elephants *Elephas maximus* and African elephants *Loxodonta africana*: underlying photoperiodic cueing?

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ABSTRACT

1. Animals in seasonal environments often rely on photoperiodicity to time their reproduction. Elephants have a gestation length of approximately two years and a historical geographic distribution including higher latitudes than at present, so the evolution of a seasonal breeding pattern cued by photoperiodicity and timed to the long-day period is a theoretical option in both species.
2. We reviewed literature on reproductive patterns in free-ranging, semi-captive and captive Asian and African elephants, photoperiodic cueing, seasonal variation in body condition, and other factors influencing their reproduction, as well as data from zoological collections on the timing of births.
3. Most of the free-ranging and all the semi-captive and captive elephant populations showed a moderate yet distinct seasonal breeding pattern.
4. Peak breeding activity of free-ranging Asian elephants took place in either the dry or the wet season, with no preference for short-day or long-day breeding at low latitudes (close to the equator) but a preference for long-day breeding at higher latitudes. Semi-captive Asian elephants mainly bred in the dry season when body condition was lowest and day-lengths were increasing. Peak conception often occurred in the wet season in free-ranging African elephants when body condition was highest, with no evident preference for short-day or long-day breeding at low latitudes but preference for long-day breeding at higher latitudes.
5. Asian and African elephants in zoos at latitudes from 43 to 53°N tended to conceive more often during spring and summer, i.e. when day-lengths were

increasing. Body condition was not reported to vary significantly throughout the year and was rather high compared to in the wild.

6. We hypothesise that elephants are 'long-day breeders' in which the photoperiodic timing of conception can be influenced by many additional factors. Strategies to encourage natural conception in captive populations should include measures aimed at increasing breeding incentives in the northern hemisphere spring.

INTRODUCTION

Long-lived mammals relying on seasonal food sources often have reproductive cycles controlled by photoperiod to ensure birthing during a time of favourable resources (Bronson & Heideman 1994, Bechert et al. 1999). Depending on whether an increase or a decrease in melatonin triggers seasonal reproduction, animals are classified as short-day breeders (autumn/winter) or long-day breeders (spring/summer; viviD & Bentley 2018). Assuming that birth in spring (during the long-day period) is desirable, and knowing the species-specific gestation length (or period), it can be predicted whether a species is a short-day or long-day breeder (Fig. 1). The evolutionary history of elephants probably included a period of adaptation to seasonal environments, as *Elephas* species ventured into Europe (Van der Made & Mazo 2003, Van der Made 2010), and the historical distribution of both *Loxodonta africana* and *Elephas maximus* spread beyond the tropics of Capricorn and Cancer, respectively (Laursen & Bekoff 1978, Shoshani & Eisenberg 1982). Based on their long gestation length of nearly two full years (Lüders 2018), one might therefore expect them to increase breeding activity in the long-day period (Fig. 1).

Many elephants kept in zoos face reproductive problems. In both species, pathologies of ovarian and uterine origin are common, as is continuous cyclicity due to a lack of breeding; acyclicity is an increasing issue, especially in reproductive-aged African females, whereas Asian females often cease reproductive activity early in life and suffer from reproductive tract pathologies affecting fertility (Dow et al. 2011, Hildebrandt et al. 2012, Brown 2014, Brown et al. 2016). Another problem is high infant mortality in captive elephant populations (Taylor & Poole 1998, Dale 2010). While the majority of publications on zoo elephants focus on acyclicity and potential causes (Yamamoto et al.

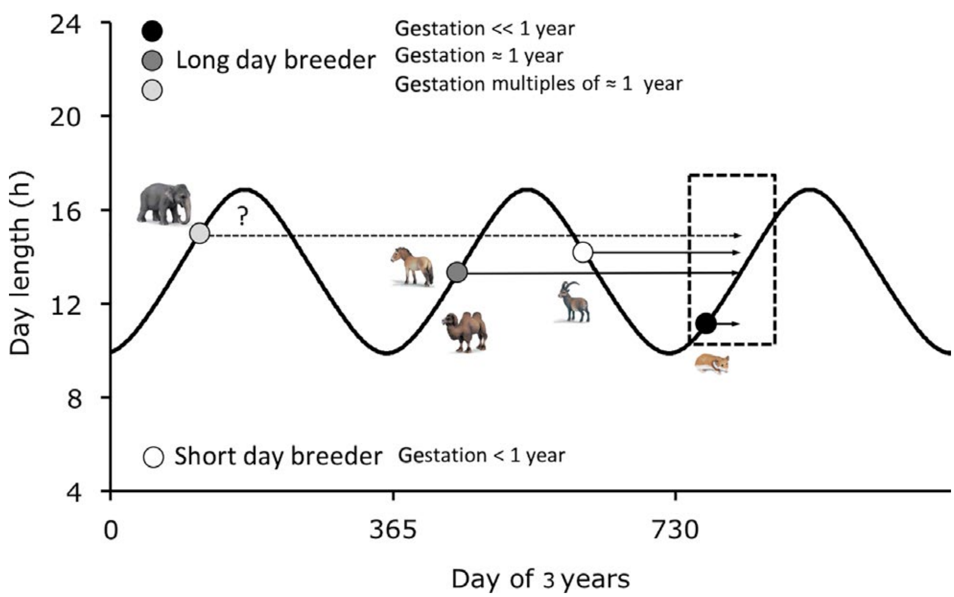

Fig. 1. Schematic concept of the interrelation between photoperiodic cueing (direction of day-length change), gestation length (arrows), and the onset of the breeding season (large black, grey and white dots). Assuming a targeted birthing season in spring (when days are getting longer, dashed rectangle), seasonal breeders with very short gestation lengths such as hamsters *Cricetus* spp. are long-day breeders with parturition in the same season (Pévet 1988), seasonal ruminants are short-day breeders with rutting in autumn and gestation lengths of less than one year (Zerbe et al. 2012), and horses (Heck et al. 2017) and camelids (Chen et al. 1985) are long-day breeders with gestation lengths of around one year. Assuming an adaptation to seasonality in elephants, they would be expected to be long-day breeders based on their long gestation length. [Colour figure can be viewed at wileyonlinelibrary.com]

2010, Glaeser et al. 2012, Brown et al. 2016), no treatment of the relevance of seasonal reproduction or photoperiodic cueing in elephants exists, to the best of our knowledge (Brown 2014).

We reviewed the literature on the seasonality of reproduction in free-ranging Asian and African elephants and evaluated data on seasonality in captive populations, assessing potential photoperiodic cueing. Additionally, we reviewed literature on other factors affecting reproduction in free-ranging and captive populations, including environmental conditions, social intraspecific interactions, and human management.

METHODS

We searched for literature on reproductive patterns, photoperiodic cueing, seasonal variation in body condition, and other factors, using PubMed and Google Scholar to detect relevant literature, as well as both literature cited in and literature citing the publications thus found. For reproductive patterns in free-ranging Asian and African elephant populations, we collected information on seasonal distribution of births or conceptions, on latitude of origin and on timing of dry and wet season from available publications and books. If there was only information on birth patterns, we calculated the respective times of conceptions, taking the Julian start day of the month mentioned as the beginning of the birth season and subtracting the gestation length, using mean lengths of 657 days for Asian elephants and 641 days for African elephants (Lüders 2018), corresponding to approximately 23 months; evaluations based on minimum and maximum reported gestation lengths (Asian elephant: 617 and 693 days; African elephant: 624 and 667 days) are given in Appendix S1. Our approach may yield results that differ from those in studies that assume mean gestation lengths of 20 months or 600 days (e.g. Joshi et al. 2009). The latitude of origin was either given in the publication or was retrieved with Google Latitude Finder (http://www.latlong.net/) by inserting the location of each study. Information about timing of the wet and dry season was either obtained from the same source, or from other publications relating to the same area. Published data were read from graphs using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/).

To assess whether elephants rely on photoperiodic cueing, we used the Julian start day of breeding and the latitude to calculate the day-length at the onset of the breeding season for those populations for which a seasonal reproductive pattern was reported, using the model developed by Forsythe et al. (1995), and noted whether days were getting longer or shorter at that time. If the conception peak(s) were reported to start in June or December (summer and winter solstices), we allocated peaks in June to the short-day or long-day period, and peaks in December to the long-day or short-day period in the northern or southern hemisphere, respectively. If there were two peaks at different times of the year, we selected the first peak of the year as the beginning of the breeding season. To compare the day-length at the onset of breeding activity between free-ranging and captive populations, we calculated the average day-length for all free-ranging populations. Because photoperiodic signals are not very distinct close to the equator below a latitude of 11.75°N or S (Bronson & Heideman 1994), we also report whether a population reproduces in the short-day or long-day period above this threshold (i.e. further north than 11.75°N or further south than 11.75°S).

To assess captive elephants, we analysed data on births of elephants from Species360 (www.Species360.org), an international non-profit organisation that maintains a data base of wild animals held in captivity. We used the method of the Birth Peak Breadth (BPB80), originally developed to quantify the seasonality of reproduction in ruminants (Zerbe et al. 2012), to describe the degree of seasonality as the number of days in which 80% of all births occur. For the calculation of the day-length during the main breeding season, we used the first Julian day of the BPB80 and subtracted the gestation length. For zoo elephants, we set a latitude of 48°N as latitude of origin, as most Asian and African elephants are held in zoos at latitudes from 43 to 53°N.

BREEDING SEASONALITY IN ASIAN ELEPHANTS

Free-ranging elephants

Free-ranging Asian elephants are capable of breeding throughout the year, but 7 of 10 studies reviewed reported seasonal distribution or seasonal conception peaks (Table 1). Generally, available data on the timing of conceptions or births in free-ranging Asian elephants are scarce.

Two early studies stated that in Sri Lanka, near the equator, the distribution of births and conceptions does not follow a seasonal pattern, although there may not have been enough data to exclude seasonality in reproduction, as numbers of observed matings, births, and populations studied were not indicated (Phillips 1935, McKay 1973). Another early study reported conceptions to peak at the beginning of the wet season in the short-day period in Sri Lanka (Eisenberg & Lockhart 1972). Other researchers found that the peak of conceptions in Sri Lanka coincided either with the dry season in the short-day period (Santiapillai et al. 1984) or the long-day period (De Silva et al. 2013), with the wet season in the short-day period

Table 1. Distribution of conceptions and conception peaks (estimated with the mean gestation length) in free-ranging and semi-captive Asian elephants *Elephas maximus* in relation to the rainy season, the long-day or short-day period, and the working season in the timber industry

	Month													
	J	F	M	A	M	J	J	A	S	O	N	D		
Latitude	Days getting longer						Days getting shorter						*n*	Source
6.29°N					xx	xx	xx	xx					84	a
6.64°N						x	x	x	x				3	b
6.64°N	xx	xx	xx	xx	xx	xx							325	c
6.64°N		x	x		x								3	*d*
7.28°N										xx	xx		41	e
7.87°N	–	–	–	–	–	–	–	–	–	–	–	–	–	*f*
7.87°N									xx				–	*g*
7.87°N	–	–	–	–	–	–	–	–	–	–	–	–	–	*h*
10.42°N	xx	xx	xx										261	*i
11.38°N	–	–	–	–	–	–	–	–	–	–	–	–	1 pop.	j
18.79°N	xx	xx	xx	xx	xx							xx	22	+k
21.91°N	xx	xx	xx	xx									3070	*l
21.91°N	xx	xx	xx	xx									2350	*m
26.62°N	xx	xx	xx	xx	xx								51	+n
30.13°N		xx	xx	xx	xx	xx							1 pop.	o

x = most conceptions take place; xx = conception peaks or increased number of females in oestrus; – = conceptions evenly distributed; light grey squares = rainy season; dark grey squares = resting time (Feb-May; Mar 2002); *n* = number of observed births/matings/studied populations (– = number not indicated); Sources: *from timber working camps, + semi-captive, *italic = data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Phillips 1935*, *g Eisenberg & Lockhart 1972, h McKay 1973*, i Sukumar et al. 1997, j Ramesh et al. 2011, k Thitaram et al. 2008, l Mar 2002, m Mumby et al. 2013, n Baskaran et al. 2009, o Joshi et al. 2009.

(Ishwaran 1981), or with the wet season in the long-day period (Kurt 1974, Katugaha et al. 1999, Table 1).

In India, at higher latitudes, Joshi et al. (2009) found conceptions to increase in the dry season in the long-day period, whereas Ramesh et al. (2011) did not identify any seasonal distribution of births in a population living in a rather aseasonal environment (Table 1).

The day-length at the onset of breeding activity or peak reproductive activity varied from 10.7 to 12.5 h (average 11.9 h) at latitudes from 6.29°N to 30.13°N (Table 2). In 4 of 7 reviewed studies reporting a seasonal pattern for free-ranging Asian elephants, the breeding season started in the long-day period (Table 3). Counting only populations that lived at latitudes higher than 11.75°N, one free-ranging population did not show any seasonal breeding pattern (Ramesh et al. 2011) in an aseasonal environment, and the other started breeding in the long-day period which coincided with the dry season (Joshi et al. 2009, Table 1).

Semi-captive elephants

Semi-captive Asian elephants conceive all year-round, but in all studies we reviewed, a seasonal pattern of reproduction was reported (Table 1). In Thailand, at 18.79°N, Thitaram et al. (2008) reported a seasonal reproductive pattern in semi-captive elephants used for tourist riding; the peak of female oestrus was at the beginning of the long-day period during the dry season (Table 1). Dry season is the peak tourist season in Thailand (December to March).

In India, at 10.42°N, Sukumar et al. (1997) reported conceptions to occur mainly in the long-day period in the dry season in two timber camps (Fig. 2) and Baskaran et al. (2009), who studied semi-captive Asian elephants used in tourism and for patrolling in the forests, also observed seasonal breeding in the long-day period in the dry season (Table 1).

In Myanmar, at 21.91°N, Asian elephants used for work in the timber industry also showed a seasonal pattern of reproduction (Table 1). Most conceptions occurred in the long-day period during the dry season (Mar 2002, Mumby et al. 2013). The conception peak was in February, which was the end of the working season, and the breeding period lasted until shortly before the resumption of work in June (Table 1).

The day-length at the onset of breeding season or peak mating activity varied from 10.5 to 11.5 h per day (average 10.9 h) at latitudes from 10.42°N to 26.62°N (Table 2). In all of the reviewed studies breeding season or conception peaks started in the long-day period and coincided with the dry season. With the exception of the population studied by Sukumar et al. (1997), all these populations lived at latitudes further north than 11.75°N.

Table 2. Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the mean gestation length in free-ranging and semi-captive Asian elephants *Elephas maximus* at different latitudes

Latitude	Julian start day	Day-length (hours per day)	Timing	Source
6.29°N	121	12.3	L	a
6.64°N	152	12.5	S	b
6.64°N	1	11.7	L	c
6.64°N	32	11.8	L	*d*
7.28°N	274	12.1	S	e
7.87°N	244	12.3	S	*f*
10.42°N	1	11.5	L	*g
18.79°N	**335**	**11.1**	**L**	**+h**
21.91°N	**1**	**10.8**	**L**	***i**
21.91°N	**1**	**10.8**	**L**	***j**
26.62°N	**1**	**10.5**	**L**	**+k**
30.13°N	**32**	**10.7**	**L**	**l**

Sources: *from timber working camps, + semi-captive, *italic= data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Eisenberg & Lockhart 1972*, g Sukumar et al. 1997, h Thitaram et al. 2008, i Mar 2002, j Mumby et al. 2013, k Baskaran et al. 2009, l Joshi et al. 2009. bold = populations from latitudes at which a photoperiodic effect might operate.

Calculating the main breeding activity with the minimum gestation length had no relevant effect on the results; using the maximum gestation length, however, reduced the number of studies that indicated long-day breeding (Table 3), because breeding activity changed close to the equinox (Table 1).

Captive elephants

In Sri Lanka at a latitude of 6.88°N, captive Asian elephants at the Pinnawala Elephant Orphanage showed conception peaks in the wettest months from September to October in the short-day period (Pushpakumara et al. 2016).

For Asian elephants housed in zoos all over the world, the BPB80 was quite long, at 276 days, indicating aseasonal reproduction. A steady increase in conceptions was recorded from January on, with a peak in May or June; conception rates were stable throughout autumn and the lowest number of conceptions occurred in October and November. Focused on zoos at latitudes from 43 to 53°N (average 48°N), where the largest numbers of Asian elephants are held in captivity, again, more conceptions were recorded from February on, conceptions peaked both in June and again in the beginning of September, and consequently reproductive activity was low from October to January (Fig. 2). Using the first day of BPB80 as the start of the birth season, captive Asian elephants held at latitudes from 43 to 53°N (average 48°N) increased breeding activity from Julian day 73 in the long-day period onward, on average when day-length was 11.7 h. Compared to the average of free-ranging populations, they increase breeding activity earlier in the year.

BREEDING SEASONALITY IN AFRICAN ELEPHANTS

Free-ranging elephants

Like Asian elephants, free-ranging African elephants are capable of breeding year-round, but 21 of 24 studies reviewed reported seasonal reproduction or conception peaks (Table 4). Depending on the location in Africa, there are two rainy seasons (usually from March to May and from October to December) interrupted by a shorter and a longer dry season close to the equator, or one long rainy season (usually from November to April) at higher latitudes.

All studies from habitats with two rainy seasons, at low latitudes, revealed a seasonal pattern of reproduction. In one of the 10 studies, the breeding season was reported to start prior to the rainy season(s) in the long-day period (Laws 1970, Table 4). Although conception peaks varied from year to year in the study conducted by Poole (1987), the peaks started on average just at the onset of each rainy season, with the first peak of the year occurring in the long-day period. Laws et al. (1975) reported three conception peaks throughout the year, taking place just at the onset of the rainy season in the short-day period and during the dry season as well as at the end of the second rainy season in the long-day period. In 7 of 10 studies from habitats with two rainy seasons, conceptions mainly occurred towards the end of the rainy season or at the beginning of the dry season, and in 5 of 7 studies they mainly occurred in the short-day period (Table 4). Moss et al. (2011) found an association between rainfall

Table 3. Number of studies (of all studies; number in parentheses) suggesting short-day or long-day breeding activity after the calculation of the breeding season with the minimum, mean, or maximum gestation length (for the total of studies/those from latitudes further north than 11.75°N), with indication of the number of changes from short-day to long-day (S-L) or long-day to short-day (L-S) breeding, compared to the mean gestation length in free-ranging and semi-captive Asian elephants *Elephas maximus*. Sources in Table 1

Gestation length	Minimum (617 days)	Mean (657 days)	Maximum (693 days)
Short-day breeding (total/above 11.75°N)	4 (12)/0 (5)	3 (12)/0 (5)	8 (12)/3 (5)
Long-day breeding (total/above 11.75°N)	8 (12)/5 (5)	9 (12)/5 (5)	4 (12)/2 (5)
Change S-L/L-S	0/1	–	0/5

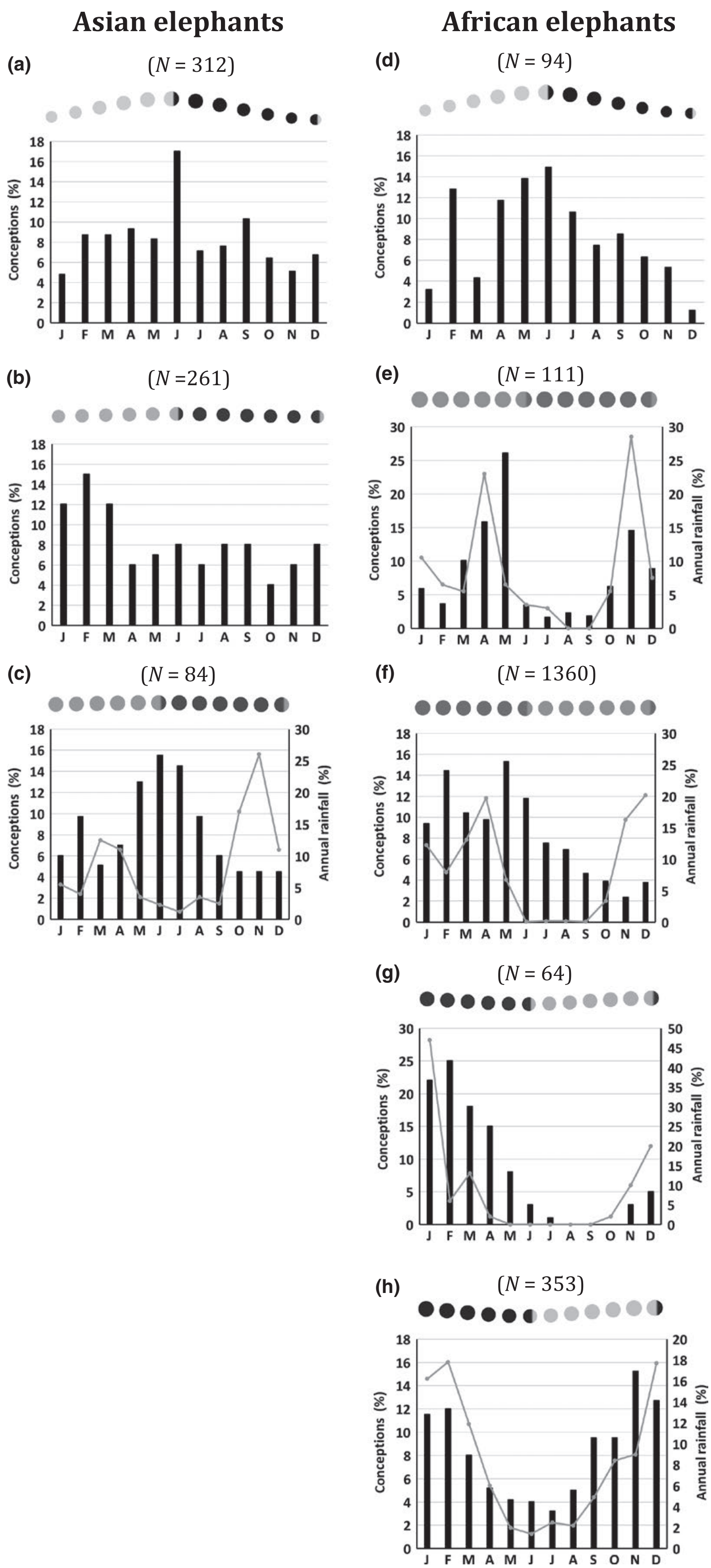
Asian elephants
African elephants
(a)
(N = 312)
Conceptions (%)
J F M A M J J A S O N D
(b)
(N =261)
Conceptions (%)
J F M A M J J A S O N D
(c)
(N = 84)
Conceptions (%)
Annual rainfall (%)
J F M A M J J A S O N D
(d)
(N = 94)
Conceptions (%)
J F M A M J J A S O N D
(e)
(N = 111)
Conceptions (%)
Annual rainfall (%)
J F M A M J J A S O N D
(f)
(N = 1360)
Conceptions (%)
Annual rainfall (%)
J F M A M J J A S O N D
(g)
(N = 64)
Conceptions (%)
Annual rainfall (%)
J F M A M J J A S O N D
(h)
(N = 353)
Conceptions (%)
Annual rainfall (%)
J F M A M J J A S O N D

Fig. 2. Monthly percentages of conceptions and rainfall (if data were available) over the year in Asian and African elephants in zoos from latitudes 43 to 53°N and in different natural habitats; short-day (dark) and long-day (light) periods are indicated by sun symbols and the extent of day-length variation over the year in the different latitudes is indicated by the different amplitudes and colour graduations of these symbols (the greater the day-length difference, the greater the contrast between dark and light), calculated with the mean gestation length: (a) captive Asian elephants in zoos from latitudes 43 to 53°N; (b) free-ranging Asian elephants, Mudumalai National Park (10.42°N), India, Sukumar et al. (1997); (c) free-ranging Asian elephants, Udawalawe National Park (6.29°N), Sri Lanka, De Silva et al. (2013); (d) captive African elephants in zoos from latitudes 43 to 53°N; (e) free-ranging African elephants, Samburu National Reserves (0.61°N), Kenya, Rasmussen (2001); (f) free-ranging African elephants, Amboseli National Park (2.65°S), Kenya, Moss et al. (2011); (g) free-ranging African elephants, Wankie National Park (18.45°S), Zimbabwe, Williamson (1976); (h) free-ranging African elephants, Kruger National Park (23.99°S), South Africa, Smuts (1975).

Table 4. Distribution of conceptions and conception peaks (estimated with the mean gestation length) by month in free-ranging African elephants *Loxodonta africana* in relation to the rainy season and the long-day or short-day period

	Month													
	J	F	M	A	M	J	J	A	S	O	N	D		
Latitude	Days getting longer						Days getting shorter						*n*	Source
2.15°N							xx	xx	xx	xx	xx		24	*a*
2.15°N	xx										xx	xx	282	*b*
1.37°N		x	x						x	x			5 pop.	c
1.37°N	xx	xx	xx									xx	31	*d*
0.61°N	x			x	x	x					x	x	203	e
0.61°N	xx			xx	xx	xx						xx	111	f
Latitude	Days getting shorter						Days getting longer						*n*	Source
0.60°S			xx					xx				xx	–	g
2.65°S	x	x	x	x	x	x						x	1030	h
2.65°S		x	x	x	x	x	x	x	x				1360	i
2.65°S	xx		xx	xx	xx	xx					xx	xx	–	j
4.00°S	x	x	x	x	x	x							82	k
4.31°S	xx	xx	xx	xx	xx	xx					xx	xx	85	*l*
9.00°S										x	x		–	m
11.91°S	x	x	x	x							x	x	179	n
13.13°S	x	x	x	x	x							x	–	o
18.45°S	x	x	x	x							x	x	64	p
19.02°S	–	–	–	–	–	–	–	–	–	–	–	–	–	q
22.33°S	–	–	–	–	–	–	–	–	–	–	–	–	–	r
23.99°S	xx	xx	xx								xx	xx	59	s
23.99°S	–	–	–	–	–	–	–	–	–	–	–	–	–	t
23.99°S	x	x	x	x							x	x	353	u
23.99°S	xx	xx								xx	xx	xx	695	v
30.56°S	x	x	x								x	x	–	w
33.48°S		xx	xx								xx		109	x

x = over 70% of the conceptions take place; xx = conception peaks or increased number of females in oestrus; – = conceptions evenly distributed; grey squares = rainy season; *n* = number of observed births/matings/studied populations (– = number not indicated); Sources: *italic = data limited; a Buss & Smith 1966, b Buechner* et al. *1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972,* m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Ansell 1960, r Smithers 1971, s Hall-Martin 1987, t Fairall 1968, u Smuts 1975, v Freeman et al. 2009b, w Craig 1984, x Hall-Martin 1987.

and conceptions, with peak conceptions occurring two months after peak rainfall.

In habitats with only one rainy season, at higher latitudes, three studies observed an aseasonal pattern of reproduction, although the numbers of observed births, matings, or populations studied were not reported (Ansell 1960, Fairall 1968, Smithers 1971). However, most (and more recent) studies reported seasonal breeding. In only one study did conceptions begin to peak before the onset of the single rainy season in the long-day period, and that peak only lasted about two months (Verheyen 1951). In 9 of 14 habitats with a single rainy season, conceptions peaked or took place from the onset of the rainy season or shortly after its onset, and in 7 of the 9 studies conceptions peaked in the long-day period (Table 4). Freeman et al.

(2009b) showed that the mean percentage of conceptions for each month was positively correlated with the mean monthly precipitation. Hall-Martin (1987) observed two conception peaks throughout the year in a population in South Africa, one just after the onset of the rainy season in the long-day period, and another towards its end in the short-day period (Table 4).

In addition to the results above, some authors not only reported fluctuations of conceptions throughout one year, but also low conception rates in years with less rain and many conceptions in years with a lot of rain in populations living near the equator (Douglas-Hamilton 1972, Moss 2001, Sukumar 2003, Moss et al. 2011).

The day-length at the onset of mating activity or peak breeding season varied from 12.0 to 13.7 h per day (average 12.4 h) at latitudes from 33.48°S to 2.15°N. In 12 of 21 reviewed studies reporting a seasonal pattern, breeding season or conception peaks started in the long-day period. Counting only populations further south than 11.75°S and reproducing seasonally, six of eight had conception peaks that started in the long-day period and at the beginning of the wet season (Table 5).

Calculating the main breeding activity with the minimum and maximum gestation length both increased the number of studies that indicated long-day breeding (Table 6), because breeding activity started to increase around the middle of the long-day period (Table 3).

Captive elephants

Apart from the data from zoo elephants below, there were few reports on seasonality of reproduction in African elephants held in zoos, but ovarian inactivity in African zoo elephants more often occurred between December and early April (Schulte et al. 2000).

For captive African elephants housed in zoos all over the world, the BPB80 was again long, at 255 days, also indicating aseasonal reproduction. An increase in conceptions was recorded from the beginning of the year on with a major peak in June, followed by a low number of conceptions for the rest of the year. Considering only the elephants at latitudes from 43 to 53°N (average 48°N), again, more conceptions were recorded from February on, with a peak in May or June and a lower number of conceptions at other times of the year (Fig. 2). Captive African elephants held at latitudes from 43 to 53°N (average 48°N) increased their breeding activity from Julian day 95 onwards in the long-day period, starting on average when day-length was 13.0 h. Compared to the average of free-ranging populations, they increased their breeding activity earlier in the year.

FACTORS INFLUENCING REPRODUCTION IN FREE-RANGING, SEMI-CAPTIVE, AND CAPTIVE ELEPHANT POPULATIONS

Photoperiod

Mammals in temperate zones usually reproduce seasonally and rely on photoperiodic cueing (Bronson & Heideman 1994). The underlying physiological mechanism is the synthesis and secretion of melatonin by the pineal gland, which peak during the night. The longer the night, the more melatonin is produced; melatonin inhibits or stimulates the reproductive axis of long-day and short-day breeders, respectively (viviD & Bentley 2018). Latitude is important for photoperiodicity; changes in day-length are more pronounced at higher latitudes. Below 30°N or S, photoperiodicity becomes gradually less useful until its value is lost in the mid to deep tropics (below 11.75°N or S; Bronson & Heideman 1994). The elephants' ancestors originated from the African continent, where they evolved in a tropical climate at latitudes near the equator

Table 5. Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the mean gestation length in free-ranging African elephants *Loxodonta africana* at different latitudes

Latitude	Julian start day	Day-length (hours per day)	Timing	Source
2.15°N	182	12.2	S	*a*
2.15°N	305	12.0	S	*b*
1.37°N	32	12.1	L	c
1.37°N	335	12.0	L	*d*
0.61°N	305	12.1	S	e
0.61°N	335	12.1	L	f
0.60°S	60	12.1	S	g
2.65°S	335	12.3	S	h
2.65°S	32	12.2	S	i
2.65°S	305	12.2	L	j
4.00°S	1	12.3	S	k
4.31°S	305	12.3	L	l
9.00°S	274	12.2	L	m
11.91°S	**305**	**12.5**	**L**	**n**
13.13°S	**335**	**12.8**	**S**	**o**
18.45°S	**305**	**12.8**	**L**	**p**
23.99°S	**305**	**12.9**	**L**	**q**
23.99°S	**305**	**12.9**	**L**	**r**
23.99°S	**274**	**12.3**	**L**	**s**
30.56°S	**305**	**13.3**	**L**	**t**
33.48°S	**32**	**13.7**	**S**	**q**

Sources: *italic = data limited; a Buss & Smith 1966*, *b Buechner* et al. *1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972*, m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Hall-Martin 1987, r Fairall 1968, s Smuts 1975, t Craig 1984. bold = populations from latitudes at which a photoperiodic effect might operate.

(Van der Made 2010). Only when ancient proboscideans had evolved a tooth structure adapted to grasses (Cerling et al. 1999) was it possible for them to disperse out of Africa into South Asia and into more seasonal regions (Van der Made & Mazo 2003, Van der Made 2010) where the evolution of a seasonal reproduction cued by photoperiodicity would have been advantageous. The absence of a common day-length linked to breeding activity (Tables 2 and 5) indicates that it is likely to be the day-length change *per se*, rather than the absolute day-length, that triggers breeding. Free-ranging Asian elephants living at higher latitudes, as well as semi-captive and captive Asian elephant populations reviewed in our study, show a moderate preference for long-day breeding (Tables 1–3). The studies reporting breeding to start in the short-day period were conducted either on populations living close to the equator or with very limited data (Eisenberg & Lockhart 1972, Ishwaran 1981, Santiapillai et al. 1984). The reviewed population of free-ranging Asian elephants living in the highest latitude increased breeding in the long-day period and in the dry season (Joshi et al. 2009), providing strong support for a photoperiodic control in elephant reproduction. Free-ranging African elephants living at lower latitudes did not show a preference for long-day or short-day breeding either, whereas most of the populations living at higher latitudes increased breeding in the long-day period (Tables 4–6). Again, studies reporting the breeding season to start in the short-day period were mostly conducted on populations living close to the equator or with limited data (Buechner et al. 1963, Buss & Smith 1966, Laws et al. 1975, Foley et al. 2001, Wittemyer 2001), or on a population without a highly seasonal breeding pattern (Moss 2001, Moss et al. 2011).

Several authors reported the occurrence of oestrus synchrony in free-ranging Asian and African elephant populations (Hanks 1972, Santiapillai et al. 1984, Sukumar 2003), and Weissenböck et al. (2009) provided the first evidence for oestrus synchrony in captive African elephants. Oestrus synchrony could be the result of a photoperiodic cue or good environmental conditions, leading to initiation of oestrus in many females at once. Other reasons for the synchronisation of oestrus in elephants could be as an antipredator strategy in order to provide protection through group defence of the calves following their mothers at heel (Santiapillai et al. 1984) or to allow the benefits of allomothering exhibited in elephant herds (Rasmussen & Schulte 1998, Moss et al. 2011).

Reliance on photoperiodic cueing could also explain why captive elephants showed rather low reproductive activity throughout winter, despite their generally high body condition. A high body condition does not necessarily mean an ideal one, as a score of 4 or 5, which is common among captive elephants, indicates overweight or even obesity (Morfeld et al. 2016). The captive populations increased breeding earlier in the year than their wild conspecifics. In domesticated farm animals such as sheep and goats (short-day breeders), simulating short days through artificial light was reported to reset the onset of reproductive activity (Chemineau et al. 2008). In horses (long-day breeders), exposure to long days through artificial light during winter also led to ovulations 2–3 months earlier than usual (Guillaume 1996). Because many captive elephants are primarily housed inside during the winter months, the influence of lengthened days due to artificial lighting could have caused a reset of reproductive activity; alternatively, the more distinct differences in day-length at higher latitudes could provide a stronger signal with an earlier effect.

Nutrition and body condition

Although Laws and Parker (1968) argued that giving birth before peak rainfall, timed by photoperiod, ensures an optimal body condition for lactating elephant cows, Ogutu et al. (2015) suggested that the food quality around the time of oestrus and mating rather than at the time of parturition is the factor which controls reproductive patterns in elephants. Supporting this, conceptions rather than births were found to be linked to local rainfall patterns by Freeman et al. (2009b). Generally, it is very difficult to disentangle the factors photoperiod and body condition from one another (Fig. 2).

The body condition of free-ranging Asian elephants in India changed significantly between the seasons, as well as the faecal glucocorticoid levels which were strongly negatively associated with the body condition score (Pokharel et al. 2017). Mumby et al. (2015b) reported

Table 6. Number of studies (of all studies; number in parentheses) suggesting short-day or long-day breeding activity after the calculation of the breeding season with the minimum, mean, or maximum gestation length (for the total of studies/those from latitudes further south than 11.75°S), with indication of the number of changes from short-day to long-day (S-L) or long-day to short-day (L-S) breeding compared to the mean gestation length in free-ranging African elephants *Loxodonta africana*. Sources in Table 4

Gestation length	Minimum (624 days)	Mean (641 days)	Maximum (667 days)
Short-day breeding (total/beyond 11.75°S)	8 (21)/2 (8)	9 (21)/2 (8)	7 (21)/1 (8)
Long-day breeding (total/beyond 11.75°S)	13 (21)/6 (8)	12 (21)/6 (8)	14 (21)/7 (8)
Change S-L/L-S	2/1	–	2/0

the same pattern for semi-captive Asian elephants in timber camps in Myanmar: the highest overall body weight was measured during monsoon months and the lowest towards the end of the dry season. By contrast, a recent study on Sri Lankan elephants found that their body condition was better in the dry season, probably because the receding water levels in reservoirs offered space for fresh grass regrowth (Ranjeewa et al. 2018). As described above, free-ranging Asian elephants at higher latitudes and semi-captive Asian elephants showed a moderate preference for long-day breeding, even though the long-day period more often coincided with the dry season when body condition was lower. The captive population of the Pinnawala Elephant Orphanage in Sri Lanka is one of the few Asian elephant populations with a preference for short-day breeding. However, these elephants live near the equator and are fed a sufficient amount of food, so matings are enabled throughout the year (Pushpakumara et al. 2016). As the quality of forage in that area was highest at the time when conceptions peak (Pushpakumara et al. 2016), it is likely that nutrition and body condition had an influence on the conception peak in this population.

The body condition of free-ranging African elephants is significantly lower during the dry season than during the wet season (Laws & Parker 1968, Foley et al. 2001). At higher latitudes, free-ranging African elephants showed a preference for long-day breeding and, although the wet season usually started in the long-day period, often together with the breeding season, many more wet months fell in the short-day period and body condition improved during the course of the rainy season (Foley et al. 2001).

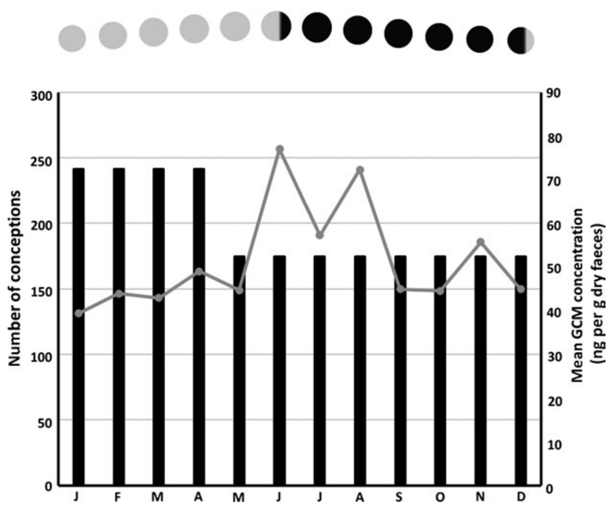

Fig. 3. Mean monthly glucocorticoid metabolite concentration (GCM) in faeces of female Asian elephants aged 17–55 years (N = 37) from timber work camps in Myanmar (21.91°N; grey line; Mumby et al. 2015a) and number of conceptions by month of timber elephants in Myanmar calculated with the mean gestation length (black bars; Mumby et al. 2013, 41% of conceptions took place from Feb to May, N = 2350, average conceptions calculated for each month). Feb-May = rest time, Jun = start of working period and monsoon (Mar 2002). For meaning of sun symbols, see Fig. 2.

For captive populations, seasonal dietary changes are not reported, and it can be assumed that captive elephants are provided with a sufficient amount of food year-round (Freeman et al. 2004). Data available from captive elephant populations in Europe indicates that there is no seasonal variation in body condition in captivity, and obesity, rather than poor body condition, is a problem (Freeman et al. 2004, Morfeld et al. 2016, Schiffmann et al. 2018). Whereas obesity in captive Asian females is not associated with acyclicity, it was found to be associated with reproductive problems in captive African elephants (Freeman et al. 2009a), although current research in zoos revealed no correlation between fat mass and cyclic reproductive activity in female African elephants (Chusyd et al. 2018). If mainly nutrition and body condition affected reproduction in elephants, we would expect captive elephants to breed completely aseasonally, due to their constantly high body condition. The fact that captive elephants start increasing their breeding activity earlier than their free-ranging conspecifics may also be an effect of their higher body condition. Seasonal ruminant species, e.g. relying on photoperiod and maintaining a seasonal pattern in captivity, start breeding earlier in the year than they would in the wild if they were in better body condition (Montgomery et al. 1985).

Intraspecific interactions

Social interactions were suspected to influence reproductive patterns in free-ranging African elephants, especially in big groups and among lower ranked elephants (Douglas-Hamilton 1972, Dublin 1983, Rasmussen & Schulte 1998, Foley et al. 2001), whereas no observations are available for free-ranging Asian elephants. Dublin (1983) found calves of dominant African elephant cows to be born earlier in the rainy season than those of subordinate females. However, Freeman et al. (2009b) did not find an association between conception month or birth month and age of the female, though age is related to social status in elephants, and Moss et al. (2011) found no evidence of reproductive suppression in animals of subordinate status either. Elephants show oestrus synchrony (Hanks 1972, Santiapillai et al. 1984, Sukumar 2003) and highly co-operative rearing behaviour. This results in larger families being more reproductively successful due to a greater number of allomothers, protectors, and older, more experienced matriarchs (Moss et al. 2011).

In captive Asian elephants, dominance rank was not reported to influence ovarian activity, whereas hierarchy was suspected to influence the reproductive state of captive African females (Glaeser et al. 2012), where ovarian inactivity was associated with a high social dominance rank (Freeman et al. 2004). Schulte et al. (2000), on the other hand, measured the longest duration of temporary ovarian inactivity or acyclicity in the most subordinate female in a captive African elephant population.

Several authors found acyclicity to be related to hyperprolactinemia (Yamamoto et al. 2010, Brown et al. 2016) and levels of prolactin were found to be positively correlated with cortisol levels in captive African elephants (Bechert et al. 1999), with high levels probably indicating social stress (Brown et al. 2016). Although free-ranging African elephants live in family units consisting of mainly related females and their offspring, female elephants in zoos are often unrelated (Freeman et al. 2004, Moss et al. 2011). Unrelated free-ranging female African elephants that were disrupted from their families had higher faecal glucocorticoid concentrations and a lower reproductive output than females in groups of relatives (Gobush et al. 2008). Additionally, captive Asian and African elephants show reduced reproductive activity in winter, suggesting that higher social stress due to closer proximity to unrelated females while mainly being housed inside during winter may influence reproduction (Schulte et al. 2000).

Another factor possibly influencing seasonal reproduction in elephants is the phenomenon of musth in males. Males in musth are more likely to breed, and were observed searching actively for females in oestrus (Poole 1989, Moss et al. 2011). In free-ranging African elephants in the Amboseli National Park, DNA analysis revealed that 74% of sires were in musth at the time of conception (Hollister-Smith et al. 2007). In a study on captive Asian elephants in the USA, no correlation between the onset of musth and the onset of oestrus was found (Duer et al. 2016), but Dow et al. (2011) measured slightly higher cyclicity rates (by approximately 11%) in female African elephants in facilities housing a bull than in those without a bull.

It is possible that contact with females in oestrus initiates the state of musth in male elephants (Poole 1989, Lincoln & Ratnasooriya 1996), or the other way around. The peak of males in musth started shortly before the peak of females in oestrus in most of the reviewed free-ranging Asian elephant populations, and a high proportion of male African elephants were in musth just at the time when many females were noted to be in oestrus (Poole 1989, Lincoln & Ratnasooriya 1996, Katugaha et al. 1999, Thitaram et al. 2008, Joshi et al. 2009, Moss et al. 2011). Musth and oestrus may occur at the same time due to favourable conditions for both, or due to a photoperiodic effect. There are very few data on the timing of musth and its influence on females in captivity; it would be interesting to investigate photoperiodic cueing in males in the future (Dow et al. 2011, Duer et al. 2016).

Other environmental stressors

In Asian elephants, heat stress was suspected to lead to delayed ovulation (Thitaram et al. 2008). Mumby et al. (2015b) measured the highest cortisol metabolite levels in semi-captive Asian timber elephants in Myanmar not during the dry season, but in the first three months of the monsoon season (June to October; Fig. 3). It is still hot at that time and the month of June also coincides with the restart of the working season after a break from February to May (Mar 2002). In many regions in Africa, temperatures reach their maximum during the rainy season, especially in January and February, and are lowest from June to October (Moss 2001, Freeman et al. 2009b, Moss et al. 2011), whereas overall cortisol metabolite concentrations were found to be highest during the dry season (Foley et al. 2001). Slightly elevated cortisol concentrations were measured in the coldest (January) and hottest (August) months in captive African elephants in a zoo in Indianapolis, USA (Brown et al. 2010).

Any kind of stress, such as high or low temperatures, high humidity or heavy workload, is likely to affect reproduction. Despite the heat and humidity, conceptions still occur or even peak in Asian elephants at the time when temperatures are highest in South Asia (Table 1). In the semi-captive working elephants, the sudden onset of intense physical workload might also explain the elevated glucocorticoid levels at the beginning of the monsoon, which could potentially cause long-term cessation of oestrus cycles in elephants (Mumby et al. 2015b). The contributions of timber work and climate to cortisol levels cannot be disentangled based on those data. However, conceptions already started to peak shortly before the work break in the long-day period in Myanmar, and in working elephants in Thailand peaks occurred in the long-day period when temperatures were high, body condition low and despite the coincidence with the peak tourist season (Thitaram et al. 2008). This can be viewed as strong support for a photoperiodic control in elephant reproduction.

The reproduction of free-ranging African elephants was not reported to be affected by heat, cold, or humidity, and the elevated cortisol metabolite concentrations measured during the dry season in free-ranging African elephants were probably caused by limited access to food and water (Foley et al. 2001). As elephants in zoos are provided with heated shelters in winter and shaded structures in summer, temperature should not have an influence on their reproduction. The reviewed data on captive Asian elephants from latitudes 43 to 53°N show that conceptions were at the lowest level in the coldest month (January) and at a low (but not at the lowest) level in the hottest month (August); conceptions in captive African elephants were at a low level in the coldest month and at a medium level in the hottest month (Fig. 2). If anything, in temperate zones cold, rather than heat, has a negative effect on reproduction, at least in captive African elephants.

Human activities can greatly influence elephant reproduction. In addition to illegal poaching for ivory, management actions such as contraception or translocations have a major impact (Dickson & Adams 2009, Owens & Owens 2009). The life and reproduction of captive elephants is almost fully controlled by human management. Access to suitable bulls is often restricted in zoo populations and the age structure of males is often not ideal for breeding. Female elephants prefer larger, older males and they also prefer males in musth (Sukumar 2003, Moss et al. 2011, Toeffels 2015). Semi-captive female elephants in Thailand are separated from males, but are exposed to them regularly at a distance. Access is provided if increased sexual behaviour is observed (Thitaram et al. 2008). In Myanmar, the timber elephants are able to socialise with camp and free-ranging elephants during the night (Mar 2002) and are held in mixed herds. Of the European institutions belonging to the European Endangered Species Program, only 44% provided their female elephants with access to a male in 2009 (Prahl 2009).

Brown et al. (2016) found that enrichment diversity and percentage of time with access to conspecifics was negatively correlated with reproductive acyclicity in zoo elephants. Enrichment through food is common in captive elephants, and is apparently presented more often during winter (Posta et al. 2013); contact with conspecifics is closer during winter when the elephants are mainly housed inside. Thus, we would expect fewer acyclic elephants at that time, which does not correspond to our findings. The most important factor for successful reproduction in captive elephant populations may be the availability of suitable males that can be given access to healthy, receptive cows at the right time (Prahl 2009, Toeffels 2015). When captive females are in oestrus, keepers usually bring them together with a bull if one is available. However, during winter when elephants are mainly housed inside, space for breeding is usually restricted. Therefore, human management might bias the apparent moderate seasonality of reproduction. The extent of that influence remains to be investigated.

CONCLUSIONS

Although Asian and African elephants are able to reproduce year-round, they show a moderate seasonal pattern of reproduction. The findings can be interpreted as indicative of an underlying photoperiod-triggered system that receives additional input from body condition and stress status. Based on our results, we hypothesise that elephants are long-day breeders. Because the photoperiod favourable for elephant reproduction in the tropics and subtropics often coincides with other seasonal triggers, such as the wet season and high body condition, it is difficult to tease these different factors apart. Elephant habitats are often characterised by rather unpredictable climatic conditions, at least in the mid- to deep tropics (as compared to more predictable temperate-zone habitats); therefore, relying completely on photoperiodicity would not be beneficial. Correspondingly, published data indicate an underlying photoperiodic influence that can be modified and even overruled by other factors.

Captive elephant populations in zoos are mainly dependent on human management. Obesity, the social composition of the herds, and the degree of enrichment diversity influence the reproductive state of individuals, and access to suitable males at the right time determines the reproductive output of females. To provide an environment that preserves and encourages a natural breeding pattern, enough free time should be provided for individuals in semi-captive working populations. For zoo elephants, the achievement of an ideal body condition, removal of possible stressors, provision of convenient enrichment, and access to suitable mates is important. We also suggest that managers of captive populations should make use of the potentially naturally occurring photoperiodic cueing, by manipulating female elephants' body condition so that it increases with increasing day-length, as well as by increasing breeding efforts by allowing contact between females and males, especially at the time of year when day-length is increasing.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Analyses of peak reproductive activity based on minimum and maximum gestation lengths, to supplement Tables 1–2 and 4–5.

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